When Refuge Becomes Risk: An Empirical Test of the Landscape of Fear Model

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ABSTRACT

The ‘landscape of fear’ has been proposed as a unifying concept in ecology by linking population distribution patterns through top-down predator-prey mechanisms. The landscape of fear predicts that prey resource selection patterns are influenced by spatially and temporally predictable patterns of predator risk across a landscape. Although the model has been suggested to predict prey space-use patterns across a variety of systems, it remains unclear if individuals exposed to similarly risky environments (i.e., within the home range) will consistently avoid predator risk. I tested the landscape of fear concept using a natural experiment where moose hunting was introduced to a previously hunter-naïve moose population. I quantified hunting risk by developing risk landscape layers derived from harvest data collected over the first three hunting seasons (2011, 2012 and 2013) in Gros Morne National Park, Newfoundland, Canada. Yearly hunter-risk layers were then used as a continuous variable in moose resource selection analysis to understand if moose respond to hunter risk, and if all individuals respond similarly to risk, as predicted by the landscape of fear. I found moose hunters were generally more likely to harvest moose near landscape features that offered easy access and a wide field of view. Moose generally did not avoid hunting risk until the second hunting season, and only during daylight hours. Conversely, at night, moose were generally found to select hunter-risky areas, with the strength of selection progressively increasing each year. I found considerable individual variation in moose response to hunting risk, however, with some individuals failing to alter selection strategies to avoid hunter risk. The motivation to respond to risk may be based on fitness related trade-offs associated with anti-predatory behavior, personality, and/or an individual’s ability to correctly assess risk on the landscape. My research highlights the importance of incorporating individual patterns in resource selection strategies when attempting to address landscape-level processes, such as the landscape of fear concept.

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DEDICATION

I dedicate this thesis dissertation to my parents, who have always provided me with never-ending love and support.

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LIST OF ABBREVIATIONS

Abbreviation	
AICc	Akaike's Information Criterion
GMNP	Gros Morne National Park
GIS	Geographic Information Systems
GPS	Global Positioning System
RSF	Resource Selection Function

INTRODUCTION

The Landscape of Fear Model

Traditional predator-prey theory has focused on quantifying the direct, lethal effects (consumptive effects; Werner & Peacor 2003; Orrock *et al.* 2008; Preisser, Bolnick & Grabowski 2009) of predators on prey population dynamics. However, recent research has uncovered the indirect or non-consumptive effects of predators on prey populations (Werner & Peacor 2003; Preisser, Bolnick & Benard 2005; Laundré *et al.* 2014). The recently popularized 'landscape of fear' has been proposed as a mechanism to describe the non-consumptive effect of predators on prey space-use patterns and fitness (Brown, Laundré & Gurung 1999; Laundré, Hernández & Altendorf 2001; Ripple & Beschta 2004). According to the landscape of fear concept, prey animals are able to detect safe and predator-risky patches across a landscape and will alter habitat selection strategies to reduce the likelihood of predator encounter (Laundré, Hernández & Ripple 2010). Predator risk avoidance often impedes optimal foraging strategies however, which may impact prey fitness and population distribution patterns (Lima & Dill 1990; Christianson & Creel 2010; Laundré *et al.* 2014).

The landscape of fear model has been proposed as a unifying concept in ecology by explaining ecosystem-level processes through top-down predator-prey interactions (Laundré, Hernández & Ripple 2010; Laundré *et al.* 2014). Although the concept has rarely been tested at the ecosystem-level (but see Fortin *et al.* 2005), the landscape of fear concept has been applied to a growing number of systems (e.g., Nicholson *et al.* 2014; Hammerschlag *et al.* 2015, Lone *et al.* 2015). In particular, the landscape of fear concept has gained popularity in Yellowstone National Park, where elk (*Cervus elaphus*) avoidance of landscape features associated with

introduced wolves (*Canis lupus*) has been implicated in shaping elk population dynamics (Ripple & Beschta 2004; Fortin *et al.* 2005; Christianson & Creel 2010). Still, the relationship between predator risk avoidance behaviour and associated fitness-costs is debated, and is difficult to quantify in nature (Middleton *et al.* 2013). For example, although roe deer (*Capreolus capreolus*) that failed to avoid hunting risk were more likely to be shot by Norwegian hunters, a number of other factors such as proximity to refugia modified the relationship between risk avoidance and the probability of survival (Lone *et al.* 2015). Despite attempts to explain population-level dynamics as a result of indirect effects of predation (Ripple & Beschta 2012), a number of other competing factors may modify the risk-response relationship predicted by the landscape of fear model.

According to the landscape of fear, prey animals are predicted to avoid predator risky patches (Laundré, Hernández & Altendorf 2001; Ripple & Beschta 2004; Laundré, Hernández & Ripple 2010). Yet, individuals within a population may differ in how they select habitat, which may result in deviations to the risk-response relationship described by the landscape of fear (Dussault *et al.* 2012; Wirsing & Heithaus 2014; Padié *et al.* 2015). Differences in individual habitat selection choices may sometimes arise as a result of fitness-related tradeoffs associated with predator avoidance behaviour (Bonnot *et al.* 2014; DeCesare *et al.* 2014). For example, individuals in poor body condition may be more likely to risk the chance of a predatory attack to gain foraging opportunities (Houston, McNamara & Hutchinson 1993; Clark 1994). Personality, as defined by consistent individual differences in behaviour (Réale *et al.* 2007), may also play a role in dictating an individual's willingness to avoid predator risk. In roe deer, an individual's willingness to confront risk (a measure of personality) can determine its probability of using risky, open habitat during the day (Padié *et al.* 2015). Despite knowledge of a variety of factors

that may affect the risk-response relationship in prey, it remains unclear if individuals exposed to similarly risky conditions will consistently avoid predator risk, as suggested by the landscape of fear model (Laundré *et al.* 2010). Rather, individuals may exhibit a high degree of variability in selection strategies when confronted with predator risk (Wirsing & Heithaus 2014; Lone *et al.* 2015; Padié *et al.* 2015). Understanding if individuals within a population consistently avoid predator risk as predicted by the landscape of fear model has especially important implications for studies attempting to address the link between risk-avoidance and fitness consequences (e.g. Christianson & Creel 2010).

The landscape of fear model has been increasingly applied to the risk effects human hunting activity may impose across a landscape (Cromsigt *et al.* 2013). Due to the nature of hunter characteristics (i.e., ability to kill at a long distance), the response of prey to hunters can be unique, and even stronger compared to other predators (Proffitt *et al.* 2009). Yet, measuring risk associated with hunting is an ideal way to test for dynamic responses in prey resource selection patterns (Lone *et al.* 2015). Human hunters can be highly effective predators and are typically the largest source of mortality in hunted systems (Cromsigt *et al.* 2013). Hunting patterns are also typically highly spatially and temporally predictable, as hunters are known to concentrate near certain landscape features (i.e., roads, trails), during daylight hours in limited hunting seasons (Lyon & Burcham 1998; Proffitt *et al.* 2010; Lebel *et al.* 2012). Accordingly, hunters are known to generate landscapes of heterogeneous, but predictable risk that prey animals are predicted to avoid (Cromsigt *et al.* 2013). Despite behaving as a model predator, relatively few studies have considered hunters risk effects on prey habitat selection responses (Lone *et al.* 2015).

Testing the Landscape of Fear Model in Gros Morne National Park

The recent initiation of hunting on a human-habituated moose (*Alces alces*) population in Gros Morne National Park (GMNP), Newfoundland, offers a unique opportunity to test the landscape of fear model on a natural system exposed to human predators. Since the establishment of GMNP in 1973, hunting has been prohibited in the Park. The introduction of human hunters to the system exposes moose to a high level of predation risk previously unencountered (wolves were extirpated in Newfoundland in the 1930s). Theory predicts this extreme variation in predation risk (from very low to very high) should elicit the greatest behavioural responses in prey (Lima & Dill 1990, Lima & Bednekoff 1999). Yet, prolonged absence of predators from an ecosystem may result in selection against sometimes costly anti-predatory behaviour (Blumstein & Daniel 2005), as has been documented with the reintroduction of wolves in Yellowstone National Park (Smith, Peterson & Houston 2003), and more recently in parts of Fennoscandia (Sand *et al.* 2006; Nicholson *et al.* 2014). However, moose are known to adjust space use patterns in response to predation risk (Neumann, Ericsson & Dettki 2009) and continued predation pressure from hunters over subsequent hunting seasons is predicted to elicit measurable behavioural responses in moose resource selection patterns. Still, it is not clear if individuals exposed to similarly risky conditions will consistently avoid hunting risk. Thus, my objective was to test the landscape of fear hypothesis that hunter predation risk would influence moose resource selection patterns over the first three years following the initiation of hunting in Gros Morne National Park, Newfoundland.

I predicted that hunter predation risk would be an important factor affecting moose resource selection patterns in GMNP (Prediction 1). As hunters are restricted to daylight hours, I expected moose to avoid hunter risk primarily during daylight hours, with the strength of the

selection weakening at night (Prediction 2). Because moose have not been exposed to hunters for over 40 years, I predicted avoidance of hunter risk will increase over successive years of hunting, as moose learn to adjust resource selection patterns to reduce the likelihood of hunter encounter (Prediction 3). Finally, I predicted that all individuals within the sample population will respond as a function of perceived hunting risk within the home range, consistent with the landscape of fear model (Prediction 4). Alternatively, individuals may show a high degree of variability in risk-response selection patterns, with some individuals failing to avoid risk as predicted by the landscape of fear.

To test my predictions it was necessary to account for individual variability in moose selection patterns, as well as to accurately quantify hunter predation risk across the landscape. Typically, animal resource selection has been quantified using resource selection functions (RSFs; Boyce *et al.* 2002; Manly 2002). Yet, resource selection function estimates only provide population-level (marginal estimate) results, or the mean response to resource variables (Gillies *et al.* 2006). Recently, Gillies *et al.* (2006) and Hebblewhite and Merrill (2008) incorporated the use of both random coefficients and random intercepts (collectively, random effects) into the traditional RSF framework. The use of random effects allows RSFs to estimate both the population-level response as well as individual's response to resource variables of interest (Gillies *et al.* 2006). For my RSF analysis I followed a mixed-model design using both random coefficients and random intercepts to quantify individual's response to human hunting risk. Despite the applicability of using the RSF mixed-model framework, few studies have incorporated the use of random coefficients in model development (Hebblewhite & Merrill 2008).

Most research studying non-consumptive effects of predators have relied on proxies for predation risk such as distance to anthropogenic features (Proffitt *et al.* 2010), or open areas (Padié *et al.* 2015). Recently, however, Dugal *et al.* (2013) used hunter harvest data from elk kill sites to determine resource variables associated with hunter kill sites to inform disease management in southwestern Manitoba, Canada. Here, I defined predator risk following the approach of Dugal *et al.* (2013) using resource selection functions developed from moose kill sites collected in Gros Morne National Park from 2011 – 2014. Defining predator risk using moose harvest locations allowed me to spatially define resource variables associated with the risk of a moose being killed by a hunter (Hebblewhite *et al.* 2005). Landscapes of hunter risk were then used as a continuous variable in moose resource selection analysis. It is important to note that I was not able to quantify the spatial risk of hunter encounter by moose, which may underrepresent hunter risk across the landscape (Hebblewhite *et al.* 2005). Despite this, moose were still expected to demonstrate a measurable avoidance of resource variables associated with hunter kill sites over the three year study period.

METHODS

Study Area

Study Area Description

The study area falls entirely within Gros Morne National Park (GMNP; 49°41′22″N 57°44′17″W), which extends over 1800 km^2 at the southern end of the Great Northern Peninsula on the West Coast of Newfoundland, Canada. The study area is characterized by 2 distinct ecoregions: the Northern Peninsula; and the Long Range Barrens. The Northern Peninsula ecoregion, often referred to as the lowlands, is influenced by Gulf of St. Lawrence weather patterns which produce cool summers and mild winters, with annual precipitation levels between 1200 –1450 mm (Banfield & Jacobs 1998; Damman 1983). The region is dominated by balsam fir (*Abies balsamea*) forests interspersed with networks of bogs, varied tree height, diverse ground flora, moss ground cover, tall snags, and a high percentage of standing or fallen dead wood resulting from self-thinning and insect mortality (Damman 1983). The Long Range Barren ecoregion, or commonly, the highlands, also constitute a small portion of the study area, restricted to the tops of the Long Range Mountains at an elevation above 400 m (Meades & Moores 1994). The Long Range Barrens have a colder mean air temperature (4.5 °C) and twice the average precipitation in the form of rain and snowfall compared to GMNP lowlands (Banfield & Jacobs 1998). The region is categorized as typically being above the tree line, dominated by arctic alpine plants growing in barren soil with interspersed balsam fir forests occurring within sheltered valleys (Meades & Moores 1994).

Natural disturbance is common throughout GMNP forests, with insect outbreaks causing the most significant form of disturbance in the Park (Taylor & Sharma 2010). Defoliated forest stands typically range from 0.5 to 2600 ha in size, resulting in 7976 ha of disturbance across the

landscape (Gosse *et al.* 2011). Despite disturbance occurring naturally in GMNP, regeneration of forest stands has been severely restricted in the Park over the past several decades (Taylor & Sharma 2010). Throughout Newfoundland's Northern Peninsula ecoregion, approximately 85 % of forest stands successfully regenerate following a disturbance event (Meades & Moores 1994). In GMNP, however, less than 27% of forest stands were found to show signs of successful regeneration (Taylor & Sharma 2010). Moose over-browsing has been implicated as the primary factor preventing the natural regeneration of forest stands, which has led to the proliferation of meadows dominated by grass, invasive weeds and low density spruce in regenerating areas (Humber & Hermanutz 2011). Evidence of cascading ecosystem effects have been documented as a result of forest alteration, particularly for a number of old-growth forest specialist songbirds (Rae, Whitaker & Warkentin 2013).

Moose History in Gros Morne National Park

Moose were introduced to the island of Newfoundland on two separate occasions: one male and one female in 1878 and two males and two females in 1904 (Broders *et al.* 1999). Current estimates of moose population size on the island of Newfoundland approximate 120,000 animals (Newfoundland Department of Environment and Conservation, unpublished data, 2015). Moose were not common in the Gros Morne area until 1967 (Pruitt, unpublished report, 1967) and it was not until Park establishment in 1973 that the moose population began to noticeably increase, likely due to a lack of predation within the park (Janes, unpublished report 1977). The GMNP moose population was believed to have peaked in 1998 with an estimated population of 7377 ±1249 moose occurring at densities exceeding 5 moose/km^2 (McLaren *et al.* 2000; Parks Canada Agency, unpublished data, 2009). In comparison, moose densities throughout the rest of boreal

Canada are typically less than 0.55 moose/km^2 (Karns 1998). Moose over-browsing likely played a key role in the decline in both forest species richness and balsam fir regeneration within GMNP (Connor *et al.* 2000; Taylor & Sharma 2010; Rae, Whitaker & Warkentin 2013). In 2009 prior to the initiation of hunting, the GMNP moose population was estimated at 4,900 animals occurring at densities of 5.9 moose/km^2 in the lowlands and 1.1 moose/km^2 in the highlands (Parks Canada Agency, unpublished data, 2009). Recent aerial survey population estimates suggest the GMNP moose population has been reduced to 3400 animals, with density estimates of 3.4 moose/km^2 in the lowlands and 0.98moose/km^2 in the highlands (Parks Canada Agency, unpublished data, 2015).

Human use of Gros Morne National Park

Prior to the implementation of moose hunting in October 2011, GMNP was primarily used by non-resident tourists for recreational activity, as well as residents living in nearby enclave communities located within the Park. Domestic timber permits are also issued to Park residents in GMNP, although timber harvest occurs on a small scale with approximately 20 ha cut per year. Several hiking trails within the immediate study area are frequented by visitors during the summer months, although hiking activity substantially declines between autumn-spring. During the winter, snowmobiling is permitted in the park along designated corridors. Snowmobilers are required to adhere to the conditions of an operator's permit, which restricts both the number of snowmobilers and permissible dates for snowmobiling (Gerrow, unpublished report, 2014).

The initial moose hunting season in Gros Morne National Park began on October 11th and ran to January 8th of 2011. Season length was extended during the 2012 – 2013 hunting season to

run from October 9th – January 27th and again extended in the 2013 – 2014 hunting season from October 15th – February 2nd, with an early season beginning on Sept. 14th in the highlands. Hunting area boundaries also expanded within the park during each year of the hunt (Figure 1). The use of motorized all-terrain vehicles (ATVs) is prohibited in Gros Morne National Park by members of the public. During periods of sufficient snowfall (as deemed by the PCA), hunting of moose by snowmobile was permitted in GMNP along the designated snowmobile corridors. Unlike other jurisdictions throughout North America where hunting is typically male biased (Ginsberg & Milner-Gulland, 1994), harvest statistics in Gros Morne National Park suggest hunters do not select for either sex, or age class of moose (Perry and McLoughlin, unpublished report, 2013).

Data Collection

Hunter Harvest Data

Prior to the beginning of the hunting season in October, 2011, Parks Canada staff assembled hunter sampling kits and tools in order to obtain a wide variety of information from shot moose. Hunter sample kits were made to enable the hunter (or Park staff) to collect a variety of samples, as well as gather information on date of harvest, kill location, sex, field age, habitat type, body condition and observational fecundity information (i.e., with calf, lactating, pregnant). Samples were collected during each season from opening day until the end of the hunting season by voluntarily hunter drop off, or manual GMNP staff collection. Following voluntary hunter drop off, field staff attempted to verify the location of moose kill site locations. To improve sample size and facilitate goodwill between GMNP and resident hunters, staff drove highways 430 and 431 (only two highways in GMNP) during peak hunting hours (morning and evening) to

distribute data kits and record the location of hunters encountered. Following the first year of the hunt, Parks Canada retrieved a total of 86 samples from killed moose, including 69 kill site locations. Sampling protocol was repeated, but refined for the 2012 – 2013 hunting season to only include hair, feces and jaw samples to simplify sampling techniques (due to logistical constraints) and encourage hunter participation. Data sheets identical to the previous year were also included in hunter sample kits. Samples were collected from opening day (October 10, 2012) through to January 27th, 2013 by voluntarily hunter drop off, or manual Park staff collection. Of the 100 data kits given out throughout the 2012 – 2013 season, 64 data kits were returned that each contained useful location information (64% response rate). Sampling was repeated during the 2013 – 2014 hunting season beginning September 14, 2013 through February 2nd, 2014 and location data from 60 hunter harvested moose (60% response rate) was collected throughout the season.

Study Animals

In March, 2011, 20 free-ranging adult female moose were immobilized with a dart gun and fitted with GPS collars (Lotek Engineering Inc., Newmarket, Ontario) in lowland areas of GMNP. Animal capture and handling was conducted in accordance with guidelines of the Canadian Council on Animal Care, University of Saskatchewan protocol ID# 20110025. Collars (data stored on-board) were programmed to attempt a GPS fix at 4-h intervals and scheduled to remain on moose for a 4-year period. Throughout the study periodic monitoring was conducted to identify potential mortality signals, as well as identify approximate moose locations. One collar malfunctioned soon after deployment and was lost from analysis. Following collar drop off or animal mortality, data was retrieved periodically throughout the three year study period (Year 1

n = 19; Year 2 *n* = 11; Year 3 *n* = 7; total *n* = 19). All 2-dimensional fixes were removed from the dataset (*n* = 741) and only 3-D fixes were used in the current analysis. All GPS locations were screened for large positional outliers and positions collected within 24 h of capture (*n* = 132) were excluded. The analyses were limited to autumn and early winter (October – January), from 2011 – 2014 as this was the time frame the hunting season occurred in GMNP while moose were fitted with GPS collars. Location data were further categorized between day/night according to the mean monthly sunset and sunrise times.

Landscape Covariates

The GIS covariates used as fixed effects in moose and hunter RSF models can be found in Table 1. Habitat type was categorized based on to suit 6 major habitat types biologically relevant to moose in GMNP: balsam fir forest, mixed conifer forest (excluding balsam fir dominated stands), deciduous forest, bog, barren and disturbed forest. Habitat types were classified using a combination of the GMNP forest inventory map (Parks Canada Agency, unpublished data, 1997) and an updated forest disturbance map (Taylor and Sharma 2010). Forest inventory information was delineated using colour, 1:12,500 scale aerial photographs taken in 1995. The current accuracy of the classification of these variables is unknown. Although the forest inventory map used for analysis was outdated, the static nature of the habitat categories chosen (i.e., bog habitat is likely unchanged since 1995 in most cases), likely buffered the error associated with habitat misidentification. I classified disturbance based on up to date disturbance mapping conducted by Taylor and Sharma (2010), who used a single-image subset of two 10-m multispectral SPOT-5 satellite images recorded in 2006 (classification accuracy of 85%). There has been no major disturbance event in GMNP since that time (C. Wentzell, pers. comm., 2015). For RSF analysis

of harvest data, I collectively classified bog, barren and disturbed forest as open vegetation, as these habitat types offered hunters a wide field of view. Balsam fir forest, mixed conifer forest and deciduous forest were grouped and classified as closed vegetation as these habitat types were considered to restrict hunter's field of view. The topographic variable of elevation (*m*) was derived from a 30 m^2 resolution Digital Elevation Model (DEM; Gesch 2007). The DEM model had a mean relative vertical error of 1.64 meters (Gesch 2007). Proximity to rivers, disturbance areas and anthropogenic features (roads, hiking trails and snowmobile trails) were calculated in kilometers in GIS (Parks Canada Agency, unpublished data, 1997). The accuracy of these variables is unknown, although likely remain highly accurate since the time of classification given the static nature of these features in the park. GPS collar locations were classified as being either in (1) or out (0) of the hunting area during the hunting period. Hunter kill site locations were classified according to the region they hunted in the park. For moose RSF analysis, I incorporated a hunter risk covariate which was developed from kill site resource selection values. Each covariate was attached to spatial location data using ArcGIS 10.1 (ESRI Inc., Redlands, California). I excluded correlated variables in RSF model analysis that were greater than r^2 = 0.8. To avoid collinearity, I excluded models that had a variance inflation factor greater than 5 (Hosmer & Lemeshow 2000).

Statistical Analysis

Resource Selection Function Analysis

A common tool for quantifying animal resource selection is the resource selection function (RSF; Boyce *et al.* 2002; Manly 2002). Using binary logistic regression, resource selection functions are used to estimate the relative probability of selection by organisms for any specified

resource unit across a defined landscape (Boyce *et al*. 2002). Resource units can constitute any point on a landscape, and site attributes (covariates in statistical analysis), such as vegetation indices or distance to features of interest (i.e., roads), can be associated with that point (Boyce *et al.* 2002). Studies that use animal GPS collar data in analysis typically follow a use/available design (Johnson 1980; Boyce *et al.* 2002; Manly 2002) where used locations (GPS fixes) are compared to an equal number of available points randomly generated within a scale of interest (i.e., home range). With the aid of statistical modelling, the relative strength of selection or avoidance for any given resource can be estimated (β –coefficient) and the proportional probability of selection of an area can be mapped using a geographic information system (Boyce *et al*. 2002).

To model hunter and marginal (population) relative moose resource selection patterns in Gros Morne National Park, I created RSFs following a use/available design using the binomial logistic regression equation:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad \text{(eqn 1)}$$

Where *w(x)* is the relative probability of selection as a function of covariates χ_1 to χ_k and β_1 to β_k are the values of resource selection coefficients estimated from fixed-effects logistic regression. Biologically plausible combinations of covariates were constructed as candidate *a priori* models (Table 2 and Table 4) and compared to one another using an information theoretic approach (Burnham & Anderson 2002). Both hunter and moose model selection was conducted using Akaike's Information Criterion (AICc), with lowest Δ AICc (i.e., < 4) values indicating more plausible model explanation (Burnham & Anderson 2002; Manly 2002). Model averaging using

Akaike weights was used for all models with a Δ AICc < 2 to estimate the most parsimonious overall model (Akçakaya 2000; Burnham & Anderson 2002; Manly 2002). In moose model selection, once the best model was determined the random coefficient for hunting risk was added to the model and AICc values were compared to previous naïve (without hunting risk coefficient) models. I calculated the conditional coefficient of determination (R^2C) in moose and hunter RSF analysis to illustrate the variance explained by each model (Table 2 and Table 4). The conditional coefficient of determination is interpreted as the variance explained by both fixed and random factors (i.e., the entire model) and was calculated in the R package MuMin (Barton 2015) following methods developed by Nakagawa & Schielzeth (2013). The top model for each RSF was then evaluated using the *k*–fold cross validation method suggested by Boyce *et al.* (2002). Presence data were randomly divided between 5 equal bin ranks. Four bins (80 % of the data) were designated as a training set and the remaining bin (20 % of the data) was designated as the validation set. Cross-validated Spearman-rank correlations (r_s) were then used to compare RSF coefficients from the training set to the validation set. Models with good predictive ability have a high, positive cross-validated Spearman rank correlation value (r_s) on a scale of –1 to 1. Mapping population-level (marginal) RSF values for hunters and moose across GMNP was done in Arc MAP 10.1 (ESRI Inc., Redlands, California) solving for equation 1 based on the top model selected (Manly 2002). RSF maps were each scaled between 0 and 1, using the normalization equation:

$$\text{Normalized } (z_i) = x_i - \min(x) \,/\, \max(x) - \min(x)$$

Where $x = (x_1, \ldots, x_n)$ and z_i is normalized data for i^{th} data. The resulting maps illustrate the relative probability of selection for resource units across GMNP by the moose population during the hunting seasons from 2011 – 2014 (Figures 10 – 12).

Quantifying Hunting Risk in Gros Morne National Park

I constructed landscapes of predation risk in Gros Morne National Park using resource selection functions (Manly 2002) developed from hunter killed moose location data. The purpose of constructing moose kill site RSFs was to create a hunter risk layer that modelled the relative probability a moose would fatally encounter a hunter at a given location. Hunter kill site selection was considered at the landscape scale, or second order of selection according to Johnson's (1980) scales of selection. I chose this spatial scale to incorporate the entire hunting area which was available to hunters. The values from each yearly hunter kill site RSF model were mapped across the Gros Morne landscape to create resource selection function relative probability maps (Figure 2). To capture predator (hunter) and prey (moose) resource selection dynamics over the three study years, I took a novel approach by adding hunter kill site RSF landscape values calculated from the previous hunting season to the following year. RSF values created for Year 1 of hunting were added to RSF values created for Year 2 of hunting. This was done to represent risk generated in a given year while maintaining residual levels of risk from the previous year. For example, a risky landscape feature defined in Year 1 is predicted to maintain some degree of risk to a moose the following year (i.e., risk lag effect; Frair *et al.* 2007), even if hunters no longer select that landscape feature to kill moose. By building on previous years risk values, I accounted for residual risk that may be associated with an area. Each hunter risk layer was then included as a covariate in moose resource selection function analysis for that corresponding time period.

Quantifying the Marginal (Population-level) Response of Moose to Hunter Risk in Gros Morne National Park

To quantify moose marginal (population-level) resource selection responses to hunting risk, I used resource selection functions following methods described for equation 1 above. Moose GPS collar data were divided according to the hunting season for each year (Year 1, 2 or 3) and time of day (day/night) to evaluate predictions 2 and 3. RSFs were then modeled according to day and night over each of the three years of study. Moose marginal resource selection function analysis followed a use-availability RSF design (Manly 2002) corresponding to a within home-range analysis, or, third order scale of selection (Johnson 1980). A within-home range scale of analysis was chosen because moose were expected to adjust resource selection patterns in response to hunters within their home range, and not across the landscape. As each moose was expected to perceive hunting risk differently based on the relative amount of risk available within their home range, I standardized risk values within the home range from 0 – 1 using the normalization equation defined above. Moose home range was calculated using the fixed kernel utilization distribution method in the Geospatial Modelling Environment (Beyer, Jenness & Cushman 2010) with Gaussian (Bivariate normal) distributions. A 95 % isopleth was used to delineate the boundaries of the home range (Vander Wal & Rodgers 2012).

Quantifying Individual Variation in Moose Resource Selection Patterns

To accommodate differences in individual moose exposure to hunting risk and predict individual variation in response to risk (P4), equation 1 was built to include random effects following methods described by Gillies *et al.* (2006) and Hebblewhite & Merrill (2008) in equation 2

below. The response to hunter risk was predicted to vary for each individual moose, therefore, the logit model *w(x)* was estimated for location *i* for individual moose, *j*, following the equation:

$$w(x) = \beta_0 + \beta_1 x_{1ij} + \gamma_j + \gamma_j x_{ij} + \ldots + x\beta \qquad \text{(eqn. 2)}$$

where β_0 is the fixed effect (mean) intercept, x are covariates with fixed regression coefficients β, γ_j is the random intercept (moose ID), and $\gamma_j x_{ij}$ is the random coefficient for hunter risk at location (i) for individual animal j. Equation 2 follows the same formula as the general RSF calculation shown in equation 1, except random intercept and coefficient terms are added to account for variation between individual animals (Gilles *et al.* 2006; Hebblewhite & Merrill 2008). Including the random intercept term (moose ID) controls for spatial and temporal autocorrelation, whereas the random coefficient (γ_j) allows for variability in the coefficient of interest by each intercept (Gilles *et al.* 2006). My notation for random effects follows Gilles *et al.* (2006) and Hebblewhite & Merrill (2008). To identify variation in individual moose response to hunting risk, the hunter risk covariate was included as the random coefficient term. This allowed me to estimate each individual's response to hunting risk. For all RSF analysis I used the lme4 package (Bates *et al.* 2013) implemented in R (R Core development Team 2013). To facilitate model convergence, each continuous variable was scaled by 2 standard deviations following methods described by Gelman (2008).

To test for individual variation in moose selection patterns (P4) I plotted moose-specific hunting risk coefficients derived from equation 2 (as the dependent variable) as a function of hunting risk in that individual's home range (as the independent variable) in Figure 6.

Coefficient estimates were derived from the top RSF model for each time of day and year. The average value of hunting risk in each moose home range was derived from the hunting risk covariate applied across the landscape for the corresponding year.

I estimated both the individual- and population- level relative probability of selection (P_{Select}) for a given resource unit based on the top RSF model for each year and temporal (day/night) period. For population level inferences I held all fixed effect variables constant at their mean, except for hunting risk and solved equation 1. The probability of selection for a resource unit was then plotted as a function of hunting risk (Figure 5). To compare population- and individual- level risk response estimates, I plotted all individual and population β risk values in Figure 6. To understand individual differences in resource selection strategies in response to hunting risk, I held all fixed effects constant at their mean except for hunting risk and solved equation 2, allowing individual responses of moose to vary with hunting risk. Probability of selection values were then plotted as a function of hunting risk encountered by each individual moose within their home range (Figures 7 – 9). Hunting risk values were restricted to the 95 % confidence interval to illustrate the most common range of risk encountered by individual moose within their home range. Due to differences in availability in covariates (i.e., hunting risk) across years and time periods, differences observed in probability of selection were not directly compared; rather, differences in direction (selection or avoidance) and ranking of coefficients were focused on.

RESULTS

Quantification of Hunting Risk in Gros Morne National Park

Moose harvest location data from a total of 193 hunter killed moose were collected from hunters between 2011 – 2014, with n = 69, 64 and 60 locations retrieved in 2011 – 12, 2012 – 13 and 2013 – 14, respectively (Figure 1). Clusters of samples collected changed throughout the park from year to year, likely due to new hunting opportunities opened in GMNP during the study period (Figure 1).

Hunter kill site resource selection patterns over the first three hunting seasons in GMNP (2011 – 2014) exhibited between-year variation although general trends were evident for all three years of study. For each of the three hunting seasons the top RSF model included the covariates: roads, open habitat types, disturbance and snowmobile trails (Table 2). Elevation was excluded from analysis due to high collinearity with roads ($r > 0.8$). Model averaging was used for all models with Δ AICc < 2 for each of the three years of analysis. The strength of selection for habitat variables differed between each of the three years of hunting (Table 3). During Year 1 (2011 – 2012 season), the top model (Δ AICc = 0) suggested hunters positively selected to kill moose in disturbance, the interaction between roads and open vegetation, snowmobile trails while avoiding rivers. During Year 2 of hunting (2011 – 2012), coefficient estimates suggested hunters selected to kill moose near roads, open vegetation, disturbance, snowmobile trails and again avoided rivers. During Year 3 of hunting (2013 – 2014), the top model indicated hunters selected to kill moose near roads, snowmobile trails, disturbance sites, open habitat types and avoided rivers. Coefficient estimates of all distance covariates that are presented in Table 3 and Table 5 illustrate the relationship between the direction of selection (positive or negative) as a function of distance moved away from the "distance to" covariate. As an example in Table 3,

hunter kill sites were estimated to have a negative relationship as distance to road increases. In other words, hunter kill sites were positively associated with close distances to roads.

Resource selection function relative probability maps for hunter kill sites were created for all hunting seasons to illustrate changes in hunting patterns in GMNP (Figure 2). Previous year hunter kill site RSF maps (t) were added to the following year ($t + 1$) to represent the additive perceived risk across the landscape, as risk in an area was expected to remain during the following year. Hunter kill site resource selection function maps were used as landscape covariates (hunting risk variable) in moose resource selection function analysis during the corresponding year.

Quantification of Moose Resource Selection Functions

Modelling marginal (population-level) resource selection functions

A total of 21,764 GPS location points were used in moose RSF analysis between 2011 – 2014 with 5,015 during the day and 5,068 points recorded at night of Year 1 (n = 19 adult female moose); 3,543 and 3,584 during day and night in Year 2 (n = 11 moose); and, 2,267 and 2,287 points taken during day and night of Year 3 (n = 7 moose). Moose GPS collar locations throughout the 3-year study period can be found in Figure 3. One moose (collar ID# 145) was confirmed to be killed by hunters in 2011 – 2012, two moose in 2012 – 2013 (collar ID # 155, 85) and one moose in 2013 – 2014 (collard ID# 45). Throughout the three year study period the proportion of time spent in or out of the permissible hunting area changed throughout the years.

Resource selection function models revealed noticeable differences in population-level resource selection patterns between day/night, and across years for moose in GMNP. Across all

seasons and years, the inclusion of the hunting risk random coefficient was included in the top model and dramatically improved model fit over naïve (without random coefficient) RSF models (Table 4). After the top model, there was considerable variation in model ranking across years and time of day. During Year 1, the model which included the interaction between hunting risk and whether or not a moose was in/out of the hunting area resulted in a variance inflation >5 and therefore was not considered in model selection. However, during Year 2 and Year 3, interacting hunting risk with whether a moose was in/out of hunting area substantially improved model fit (Table 4). Spearman rank coefficient scores developed from *k*-fold cross validation were high (>0.8), indicating good model fit across top models.

The habitat covariates predictive of moose population-level resource selection patterns varied across yearly and day/night models (Table 5). During the day of Year 1 of hunting, moose strongly avoided bog and barren habitat while also avoiding rivers, hunter killed moose locations, elevation and disturbed habitat. There was weak selection for mixed conifer forest and hunting risk. Balsam fir and deciduous forest as well as distance to snowmobile trails were dropped in the final model. At night during Year 1 of hunting, moose continued to strongly avoid bog, although barren was only weakly avoided. Moose selected disturbance, rivers and hunting risk. Balsam fir, deciduous forest, mixed conifer forest, elevation and distance to hunter killed moose locations and snowmobile trails were dropped in the final model. Daytime models from Year 2 of hunting suggest moose selected balsam fir, deciduous forest and disturbance while strongly avoided hunting risk when in the hunting area as well as bog, and barren habitats. Mixed conifer forest, elevation, distance to snowmobile trails, and hunter killed moose locations were excluded from the final model. Nighttime models from Year 2 of hunting indicate moose selected for disturbance, balsam fir, and rivers. Moose also strongly selected hunting risk while

in the hunting area. Once again model estimates indicate moose strongly avoid bog and barren habitat types. Balsam fir forest, deciduous forest, elevation and distance to hunter killed moose locations and snowmobile trails were dropped in the final model. During the day of Year 3, top model coefficients suggest moose strongly avoided bog and barren and generally avoided proximity to hunter killed moose locations, mixed conifer forests, balsam fir forest, snowmobile trails and high elevation. Moose also avoided hunting risk when in the hunting area. Deciduous forest, disturbance, and distance to rivers were excluded from the final model. At night of Year 3 of hunting, moose once again strongly avoided bog and barren. Mixed conifer forest, balsam fir forest, proximity to hunter killed moose locations, high elevation and snowmobile trails were avoided. Moose strongly selected hunting risk while in the hunting area. Deciduous forest, disturbance, and distance to rivers were excluded from the final model. Distance to roads was highly collinear with elevation for all models; therefore, roads were excluded from moose RSF analysis.

Marginal selection coefficients for hunting risk estimated from day- and night- yearly resource selection functions varied, although moose generally avoided hunting risk during the day and selected hunting risk at night across years (Figure 4). To understand if moose probability of selection was a function of hunting risk, all landscape covariates were held constant except for hunting risk, and equation 2 was solved for each top RSF model (Figure 5). During the day, moose probability of selection generally declined as a function of hunting risk, with the slope of the response peaking in Year 2 of hunting. This suggests moose with a highly risky home range had a higher degree of avoidance for hunting risk compared to moose with a low risk home range. Generally at night, moose probability of selection of an area increased as a function of hunting risk, with the magnitude of response increasingly progressively with years of hunting.

Resource selection function relative probability maps were made to illustrate difference in moose population-level selection patterns throughout the study period (Figures 10 – 12).

Modelling conditional (individual-level) resource selection functions

There was considerable variation in hunting risk selection coefficients estimated between individual moose, and individuals varied according to time of day and year (Figure 6). Moose individual coefficient estimates for hunting risk also varied considerably from the population coefficient estimates for both day and night across all years, although no consistent patterns in individuals response to hunting risk were evident based on the amount of hunting risk in the home range (Figure 6). Individual moose with higher risk levels within their home range generally exhibited greater differences between day and night coefficient estimates although this trend was not consistent for all moose.

Conditional probability of selection predictions were estimated for each moose to highlight differences in selection patterns to hunting risk by holding all variables constant, except hunting risk and solving equation 2. The magnitude and direction of the predicted response to hunting risk differed considerably between moose, although there was no consistent pattern evident among individuals (Figures 7 – 9). As I centered ($\bar{x} = 0$) and standardized my random coefficient values (Gelman 2008), my random coefficients followed a normal distribution curve supporting the assumption of normality at the individual moose level.

DISCUSSION

General Discussion

Prey populations are known to adjust resource selection strategies to minimize the likelihood of predator encounter across a variety of systems (Creel *et al.* 2005; van Beest *et al.* 2013; Padié *et al.* 2015). The landscape of fear model predicts that prey animal's should adjust resource selection patterns as a function of perceived predator risk, as failing to avoid predators can be detrimental to fitness (Cresswell, Lind & Quinn 2010; Laundré, Hernández & Ripple 2010). Yet, it remains unclear if individuals exposed to similarly risky environments consistently avoid risk, as predicted by the landscape of fear model. Here, I tested the landscape of fear concept in a natural system where moose have recently been exposed to human hunters. My objectives were to understand if moose responded to hunter risk consistent with the landscape of fear model, and if so, would individuals consistently avoid hunter risk as a function of risk within the home range. My research reveals that, although hunter risk may affect prey resource selection strategies, the risk-response relationship is complex and often inconsistent with the landscape of fear model. This study highlights the importance of incorporating individual patterns in resource selection when applying the landscape of fear model to study systems.

I found risk from human hunters to be an important factor influencing moose resource selection patterns at the population-level in Gros Morne National Park (Prediction 1). Hunters were found to consistently kill moose near roads, disturbance sites, snowmobile trails and open areas across all three years of study (Figure 2). This regularity in harvest patterns resulted in a landscape with spatially and temporally predictable landscapes of risk, which is a requisite condition of the landscape of fear model (Cromsigt *et al.* 2013). By Year 2 of hunting in Gros Morne, my results suggest moose were generally able to perceive heterogeneities in hunting risk

across the landscape and adjust resource selection patterns accordingly. However, moose response to risk was complex and varied among individuals, time of day, and it was dependent on whether or not individuals were in hunting area boundaries.

Moose were generally found to differ in the how they selected for risky habitat between day and night, and across years (Predictions 2 & 3). During the day, moose risk-response estimates at the population-level support the landscape of fear model, as moose generally decreased selection for an area as hunting risk increased (Figure 5). At night, however, moose were generally found to select for hunter risk (Figure 4). During Years 2 and 3 of hunting, moose response to hunter risk was dependent on whether or not they were in the hunting area, as individuals strongly avoided hunting risk only when they were in hunting area boundaries. The ability to correctly identify refuge boundaries to avoid hunters is documented in a variety of ungulates across a number of systems (e.g., Tolon *et al.* 2009; Brook 2010; Cromsigt et al. 2013), but to my knowledge this is the first study to demonstrate this behaviour in moose. Although moose generally responded to hunting risk at the population-level, at the individual-level, there were no apparent patterns between the probability of selection for an area and the amount of hunting risk in that area (Figures 7 – 10). Rather, individuals differed in the direction and magnitude in their response to hunting risk, which often varied among individual moose and within individuals across time periods (Figures 7 – 10). In many cases, individuals did not avoid hunting risk while living in a highly risky environment, inconsistent with the landscape of fear model (Prediction 4; Figure 6). These results highlight the challenge of generalizing the effect of predator risk across prey populations, as often described in landscape of fear literature (e.g., Christianson & Creel 2010). An animal's decision to respond to risk may depend on a complex suite of biological conditions (i.e., body condition; Houston, McNamara & Hutchinson 1993),

abiotic factors (i.e., snow depth; Kittle *et al.* 2008), and even individual personality (i.e., bold vs. shy; Cuiti *et al.* 2012).

The complex response of moose to hunting risk observed within this study may partly be explained by fitness-related tradeoffs associated with risk avoidance strategies. Predator-prey literature often asserts that prey animals commonly face a trade-off between predator avoidance behavior and other fitness-related activities, such as foraging (Lima & Dill 1990; Lima & Bednekoff 1999; Brown & Kotler 2004). Differences in moose selection patterns observed within this study may be indicative of a tradeoff between predator avoidance and foraging requirements. Moose generally avoided hunter risk during the day, although hunter risky areas were selected at night, with the strength of selection increasing progressively over the years (Figure 5). As hunting is prohibited at night in GMNP, moose correctly identified the temporal predictability of hunter risk in those areas. Temporal shifts in selection patterns to avoid human hunters in forage rich areas is a phenomenon documented throughout ungulate literature (Godvik *et al.* 2009; Lone *et al.* 2015; Padié *et al.* 2015). In this study, two hunter risky areas in particular, disturbance areas, and roads, are known forage-rich attractants to moose in GMNP. For instance, moose have previously been described to select disturbance areas in Gros Morne National Park lowlands, as these areas contain regenerating vegetation preferred by moose (Kerckhoff *et al.* 2013). Further, moose are known to be attracted to roadside vegetation throughout Newfoundland (Joyce & Mahoney 2001). Still, not all moose displayed a temporal shift in selection patterns in response to risk. Some individuals consistently avoided risk day and night, while others selected for risk during the day while avoiding these areas at night. This finding suggests forage-related tradeoffs may not be the only factor influencing moose selection strategies (Figure 6). The wide range of selection patterns observed in risky areas may be

explained by some individual's inability to detect and correctly assess either the temporal predictability in risk, and/or their current exposure to risk in an area (Padié *et al.* 2015).

Resource selection studies often convey the idea that highly selected areas or resources result in higher fitness potential for individuals (reviewed in Gaillard *et al*. 2010). Some studies have been successful in illustrating the link between fitness measures and selection. For example, McLoughlin *et al.* (2006) illustrated that selection for *Agrostis/Festuca* grassland resulted in higher lifetime reproductive success for roe deer on the Isle of Rum. Recently, Lone *et al.* (2015) showed that red deer that survived the hunting season in Southern Norway were more likely to select dense cover habitat compared to individuals that were shot. Although I did not link moose selection strategies with fitness-related trade-offs at the population-level, several moose observed in this study highlight the link between selection and survival. For example, moose ID# 85 selected hunter-risky areas during the day in Year 2 of hunting and was known to be killed by a hunter during the season (Figure 8). Moose ID# 65, which lived throughout the entire study period, consistently avoided hunters during the day for all three hunting seasons (Figures 7 – 9). These individuals would conform to fitness-related assumptions made under the landscape of fear model, in that risk avoidance (or failure of risk avoidance) is correlated with fitness outcomes (e.g., Creel *et al.* 2007). Yet, moose ID# 75 which consistently selected hunting risk during the day when the probability of being shot was high, also lived throughout the study period (Figure 7 – 9). This result highlights a break down between selection and survival (e.g. DeCesare *et al.* 2014) which can be problematic for studies that assume fitness is conveyed through resource selection (Gaillard *et al.* 2010).

Most habitat selection studies do not incorporate individual patterns of selection in model analysis (except see, Dussault *et al.* 2012). I was able to effectively demonstrate differences in

individual habitat selection patterns using a traditional RSF approach by incorporating random effects in model development. Although several authors have advocated for the use of random effects in RSF analysis in the past (Gilles *et al*. 2006; Hebblewhite & Merril 2008), there are still few studies that have taken advantage of this approach. Using mixed-models with random terms allows for both marginal (population) and conditional (individual) estimates to be calculated, which is useful for making both population- and individual- level inferences and comparisons. Perhaps the greatest benefit of the mixed-modelling approach is that by including a random intercept term along with a random coefficient term for a habitat variable of interest (i.e., risk) one is able to isolate an individual, or group, response to that particular habitat variable (Hebblewhite & Merrill 2008). In this study, I was able to recognize an individual's response to hunting risk by including individual moose ID as the random intercept and hunting risk as the random coefficient term. Including hunting risk as a random coefficient term also improved model fit considerably (Table 5), resulting in more accurate coefficient estimates. Incorporating random effects into resource selection analysis studies is a relatively simple way of identifying individual variation in resource selection patterns. This approach may be particularly valuable for studies testing differences in fitness outcomes as a result of individual habitat selection strategies.

Using mixed-models with random effects in RSF analysis is also an effective way to identify specialization in resource selection patterns within populations of animals. There may be many optimal foraging strategies for individuals within a population (Pyke 1984), yet using the traditional RSF framework only the mean response of populations to resources is estimated. Using a traditional RSF approach without random coefficient terms we are only able to interpret the mean population response to resource variables, which may eclipse unique or distinct groups

of individuals within a population (McLoughlin et al. 2010). Recognizing individual or group responses to certain stressors (i.e., agricultural development) should be considered in any study of habitat selection as it provides information on the mechanics underlying population-level outcomes.

Defining predator risk was central to my study as I was interested in understanding the risk effects of hunters on moose resource selection patterns. Most studies applying risk effects at the landscape-level rely on anecdotal proxies for predator risk, such as roads (e.g., Proffitt *et al.* 2010), or open areas (Padié *et al*. 2015). I quantified hunter risk in GMNP by using resource selection functions based on moose kill sites, similar to methods conducted by Dugal *et al.* (2013). Hunter kill site resource selection layers were used as a continuous risk landscape variable in moose RSF analysis, allowing me to account for risk across the landscape at a given time. I found moose hunters consistently killed moose near roads, snowmobile trails, disturbance sites and open areas, although the magnitude of selection for each variable changed from year to year (Table 3). To account for temporal differences in hunter success for these variables, and to include risk that would have been present in the previous year, I added the previous year's ($t - 1$) landscape of risk to current the risk (t) layer. I scaled risk across the landscape to within the home range for moose, as moose perception of risk is likely based on individual experience within the home range (Laundré *et al*. 2010; Padié *et al*. 2015). By integrating residual levels of risk from previous years in model analysis I was able to account for both spatial and temporal patterns in risk according to changing harvest patterns.

Predator-prey dynamics have been described as a constant struggle between two equally armed combatants (Brodie 1999). Gros Morne National Park was a model system to illustrate the dynamic predator-prey game between moose and moose hunters. Failure to avoid hunters

increased the probability of death for at least some moose; failure of hunters to select areas with a high probability of moose encounter likely resulted in an unsuccessful hunt. During the first year of hunting, it appears hunters "won" the predator-prey game, as moose failed to avoid hunters, possibly due to a lag effect in predator recognition (Figure 2; 10 – 12). The first year of hunting was also a period that corresponded to high harvest success rates (>80 %) among hunters. Subsequent years, however, illustrated a noticeable change in selection behaviour for many moose, as individuals generally began to avoid hunter-risky areas across the landscape (Figure 11, 12). During this time hunters did not substantially change harvest selection patterns, and continued to select landscape features that offered easy access and a wide field of view. The difference in resource selection across the landscape ultimately suggested that moose were generally 'winning' the predator-prey game, which is substantiated by the fact hunter harvest success declined in successive years of the hunt (<60 %). Understanding potential fitness related trade-offs associated with patterns of selection in response to hunting risk would be an interesting prospect in evaluating the indirect effects of predation risk on moose population dynamics in Gros Morne National Park.

Management Implications

The introduction of hunting in Gros Morne National Park was a lesson in management, as well as research. The Parks Canada Agency initiated moose hunting in GMNP due to the landscape-scale impacts the hyper-abundant moose population was having on the parks endemic ecosystem (Parks Canada Agency, unpublished report, 2009). The effectiveness of the population reduction program was outlined by two primary objectives; vegetation recovery (relative to pre-determined monitoring targets), and the numerical decrease in moose densities equivalent to that managed by

the province of Newfoundland, of 1 – 2 moose/km^2 (Parks Canada Agency, unpublished report, 2009). Recent aerial surveys suggest that the moose population in Gros Morne National Park has declined to target objectives in some areas, and is 30 % lower compared to pre-hunt population estimates (T. Knight, pers. comm.). Harvest mortality was likely the major factor leading to the moose population decline. Despite the successful reduction in moose population density, Rettie (unpublished report, 2010) suggested that maintained hunting pressure will be necessary to suppress moose population numbers to promote vegetation recovery. Yet, as my research highlights, relying on current hunting trends to achieve vegetation recovery throughout the park may not be adequate given predictable hunter patterns and moose behavioral adjustments to avoid hunters. Over the course of the three years of analysis, hunters were successful in killing moose with landscape features that offered easy access (e.g., near roads, snowmobile trails), a wide field of view (open habitat types), and were believed to be used by moose (disturbance sites). By Year 2 of hunting, the majority of moose were found to avoid hunter-risky landscape features during the day; although selected for hunter-risky areas at night. Given that many moose have appeared to alter selection patterns to avoid hunters, and trends suggest hunters are unlikely to change hunting patterns, vegetation recovery may be slow in some areas of the park. Correlating vegetation survey results with predicted selection estimated from my RSF models would be an interesting prospect to test if moose avoidance relates to vegetation recovery. Ideally, hunting risk would become more spatially and temporally unpredictable in GMNP to prevent moose from learning how to avoid hunters on the landscape (Cromsigt *et al.* 2013). Yet, it is well understood managers are limited in their ability to direct hunting pressure, and permit hunting at night. It is still worth conveying to hunters that the probability of encountering a moose is typically highest in mature forest away from anthropogenic features (i.e., roads).

Summary and Conclusions

The landscape of fear concept predicts prey animals are able to recognize predator risk and adjust behavioral patterns accordingly. I tested the landscape of fear concept using a natural experiment to understand if risk generated by newly introduced moose hunters would influence resource selection patterns of prey moose. Over time I found moose generally learned to avoid predictably hunter-risky areas on the landscape during the day, and increasingly select these areas at night. Yet, I found considerable individual variability in resource selection patterns in response to hunting risk, suggesting the decision to respond to hunting risk may be influenced by a number of factors operating at the individual level. Previously the landscape of fear model has been suggested to predict population dynamics based on knowledge of predator-prey selection patterns on a landscape (Laundré *et al.* 2014). However, the finding that individual moose had high variability in selection patterns in response to risk leads to inconsistencies with population predictions made under the landscape of fear model. Integrating individual patterns of selection in response to risk in individual-based fitness models (e.g., life time reproductive success; McLoughlin *et al.* 2006) would provide a better understanding of population dynamics in Gros Morne National Park. Further, understanding fitness outcomes associated with unique individuals is an interesting prospect in evolutionary ecology (e.g., Cuiti *et al*. 2012).

TABLES AND FIGURES

Tables

Table 1: Description of covariates used in moose and hunter resource selection function analysis in Gros Morne National Park, 2011 – 2014. Disturbed forest classification was updated in 2006 by Taylor and Sharma (2010). Elevation was based on a 30 m^2 digital elevation map (Gesch 2007). Classification for all other habitat types were based on the 1997 Gros Morne landcover map (Parks Canada, unpublished data).

Environmental Predictor Variable	Layer Description
Balsam Fir Forest	Balsam Fir dominated forest made up various height class, age class, density and disturbance gaps.*
Mixed Forest	Site comprised of pockets of open forest (canopy < 4 m), Balsam Fir, Black Spruce, Krummholz (Tuckamore), Tamarack, White Birch, Trembling Aspen and Alder. *
Deciduous Forest	Deciduous forest made up of White birch, Trembling Aspen and Alder. >50% of ground cover; sparse forest canopy. Very little balsam fir and some scattered Black Spruce stands < 4 m in height. *
Disturbed Forest	Remnant forest canopy (< 25%) consisting mostly of birch. Ground vegetation (> 50%) is dominated by grass or ferns. Significant amounts of dead material (standing or fallen). Scattered regenerating spruce (< 6m). Balsam fir regeneration has failed or is vulnerable to failing. Classification based on Taylor and Sharma (2010), with an accuracy assessment of 85%.
Bog	Wetlands typically having a saturated water regime, and frequently covered by peat, ericaceous shrubs, sedges, and sphagnum moss. *
Barren	Barren rock or soil with less than 25% tree cover. *
Elevation	Elevation above sea level (km) based on a 30 m^2 digital elevation map. Mean vertical accuracy of 1.64m.
Distance to Hunter Points	Euclidean Distance of each fix to the nearest hunter harvest point on the landscape.*
Distance to Rivers	Euclidean Distance of each fix to the nearest river on the landscape.*
Distance to Snowmobile Trails	Euclidean Distance of each fix to the nearest snowmobile trail on the landscape.*
Distance to Roads	Euclidean Distance of each fix to the nearest road on the landscape.
Hunter Risk	Modelled continuous variable representing the relative probability of hunter selection at a given resource unit. (See Methods).
Open Vegetation	Any vegetation type considered to offer a wide field of view for hunters. Consisting of Bog, Barren and Disturbed habitat types.
Closed Vegetation	Any Vegetation type considered to not offer hunters a wide field of view. Consisting of Balsam Fir Forest, Mixed forest and Deciduous Forest.
In Hunting Area	Binary variable indicating whether or not a GPS point is found within the hunting area (1) or not (0).

* No available data on current accuracy of variable.

Table 2: Results of model selection for years 1, 2 and 3 mixed-effects resource selection models based on hunter harvest data over the first three years of hunting (2011 – 2014) in Gros Morne National Park, showing model name, structure, random coefficients and intercepts, Δ AICc and conditional coefficient of determination (R^2C) scores. Top Models are highlighted in bold.

Model Name	Structure	Random Intercept	ΔAICc	Conditional Coefficient of Determination (R^2C)
Year -1 Model				
Roads	Roads	Hunting Region	7	0.39
Anthropogenic Features	Dist. Roads + Dist. Snowmo. + Dist. Disturbance	Hunting Region	6	0.46
Natural Features	Dist. Rivers + Elevation + Open Veg.+ Closed Veg.	Hunting Region	20	0.37
Global Model	Dist. Rivers + Dist. Snowmo. + Dist. Disturbance + Closed Veg. + Dist. Roads * Open Veg.	Hunting Region	3	0.64
Top Model*	**Dist. Disturbance + Dist. Snowmo + Dist. Rivers + Dist. Roads * Open Veg.**	**Hunting Region**	**0**	**0.63**
Year-2 Model				
Roads	Roads	Hunting Region	1	0.54
Anthropogenic Features	Dist. Roads + Dist. Snowmo. + Dist. Disturbance	Hunting Region	2	0.56
Natural Features	Dist. Rivers + Elevation + Open Veg. + Closed Veg.	Hunting Region	27	0.16
Global Model	Dist. Rivers + Dist. Snowmo. + Dist. Disturbance + Closed Veg. + Dist. Roads * Open Veg.	Hunting Region	6	0.62

Top Model*	**Dist. Disturbance + Dist. Snowmo + Dist. Rivers + Dist. Roads + Open Veg.**	**Hunting Region**	**0**	**0.6**
Year-3 Model				
Roads	Roads	Hunting Region	9	0.62
Anthropogenic Features	Dist. Roads + Dist. Snowmo. + Dist. Disturbance	Hunting Region	7	0.64
Natural Features	Dist. Rivers + Elevation + Open Veg. + Closed Veg.	Hunting Region	30	0.74
Global Model	Dist. Rivers + Dist. Snowmo. + Dist. Disturbance + Closed Veg. + Dist. Roads * Open Veg.	Hunting Region	2	0.72
Top Model*	**Dist. Disturbance + Dist. Snowmo + Dist. Rivers + Dist. Roads + Open Veg.**	**Hunting Region**	**0**	**0.71**

*The top model for all three yearly RSF models were calculated using a weighted Akaikes model averaging approach.

Table 3: Model structure for the top yearly (year 1, 2 and 3) mixed-effects models for hunter resource selection based on harvest data collected in Gros Morne National Park from 2011 – 2014. β refers to model derived beta coefficient estimates, and SE is the coefficient estimates standard error. --- indicates the covariate was excluded from the top model.

	Year-1		Year-2		Year-3	
Fixed Effects	β	SE	β	SE	β	SE
Intercept	-1.01	0.778	-0.09	0.343	-0.52	0.783
Open Vegetation	---	---	-0.29	0.45	-0.13	0.386
Dist. Roads	---	---	-3.94	0.918	-4.05	1.209
Dist. Snowmo.	-1.01	0.831	-0.07	0.263	-3.55	1.122
Dist. Disturbance	-2.18	1.138	-0.19	0.486	-1.04	1.058
Dist. Rivers	0.24	0.402	0.02	0.263	2.453	0.855
Open Veg. * Roads	-2.08	1.571	---	---	---	---
Closed Vegetation	---	---	---	---	---	---
Random Effects	Variance	St. Dev.	Variance	St. Dev.	Variance	St. Dev.
γ (Hunting Region)	0.93	0.964	< 0.01	< 0.01	0.737	0.8584

Table 4: Results of model selection for years 1, 2 and 3 mixed-effects resource selection models derived from female GPS-collared moose in Gros Morne National Park between 2011 – 2014 for day and night, showing model name, structure, random coefficients and intercepts, and Δ AICc and conditional coefficient of determination (R^2C) scores. Top Models are highlighted in bold. See Appendix A for detailed list of candidate models.

Model Name	Structure	Random Coefficient	Random Intercept	ΔAICc	Conditional Coefficient of Determination (R^2C)
Year - 1 Day					
Best Naïve Model	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters	1	Moose ID	48	0.09
Best Model + Random Hunting Coefficient	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk	Hunting Risk	Moose ID	0	0.11
Best Model + Random Hunting*In Hunt Zone	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	VIF > 5	---
Year-1 Night					
Best Naïve Model	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers Hunting Risk	1	Moose ID	65	0.04
Best Model + Random Hunting Coefficient	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers Hunting Risk	Hunting Risk	Moose ID	0	0.06

Best Model + Random Hunting*In Hunt Zone	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	VIF > 5	---
Year-2 Day					
Best Naïve Model	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers	1	Moose ID	81	0.11
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk	Hunting Risk	Moose ID	35	0.12
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0	0.17
Year-2 Night					
Best Naïve Model	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers	1	Moose ID	124	0.07
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers * Hunting Risk	Hunting Risk	Moose ID	60	0.08
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers +Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0	0.17
Year-3 Day					

Best Naïve Model	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo	1	Moose ID	193	0.17
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo. +Hunting Risk	Hunting Risk	Moose ID	170	0.21
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters +Dist. Snowmo. + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0	0.4
Year-3 Night					
Best Naïve Model	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo.	1	Moose ID	125	0.15
Best Model + Random Hunting Coefficient	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk	Hunting Risk	Moose ID	105	0.19
Best Model + Random Hunting*In Hunt Zone	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0	0.23

Table 5: Model structure for the top yearly (Year 1, 2 and 3) and temporal (day and night) mixed effects model for moose resource selection estimated from GPS locations collected during the hunting season in GMNP from 2011 – 2014. --- indicates the covariate was excluded from the top model.

Year-1				
Fixed Effects	β-Day	SE-Day	β-Night	SE-Night
Intercept	0.27	0.056	0.11	0.041
Barren	-0.98	0.087	-0.49	0.0851
Bog	-1.77	0.107	-1.21	0.01
Conifer	0.01	0.059	---	---
Deciduous	---	---	---	---
Balsam Fir	---	---	---	---
Disturbed	-0.1	0.077	0.32	0.074
Elevation	-0.2	0.071	---	---
Dist. Rivers	0.24	0.051	-0.14	0.051
Dist. Snowmo.	---	---	---	---
Dist. Hunters	0.22	0.077	---	---
Hunting Risk	0.01	0.12	0.09	0.159
Hunting Risk * In Hunting Zone	---	---	---	---
Random Effects	Variance		Variance	
γ (moose)	0.01		<0.01	
γHunting Risk	0.2		0.15	
γ (Hunting Risk * Protected Area	---		---	

Year-2				
Fixed Effects	β-Day	SE-Day	β-Night	SE-Night
Intercept	-0.19	0.198	-0.2	0.198
Barren	-0.8	0.087	-0.47	0.082
Bog	-1.77	0.11	-1.25	0.093
Conifer	---	---	---	---
Deciduous	0.16	0.102	---	---
Balsam Fir	0.28	0.076	0.21	0.077
Disturbed	0.16	0.08	0.3	0.076
Elevation	---	---	---	---
Dist. Rivers	-0.19	0.06	-0.2	0.54
Dist. Snowmo.	---	---	---	---
Dist. Hunters	---	---	---	---

Hunting Risk	---	---	---	---
Hunting Risk * In Hunting Zone	-0.4	0.248	0.19	0.507
Random Effects	Variance		Variance	
γ (moose)	0.24		0.282	
γHunting Risk	---		---	
γ (Hunting Risk * In Hunting Zone	0.36		2.15	

	Year-3			
Fixed Effects	β-Day	SE-Day	β-Night	SE-Night
Intercept	0.71	0.155	0.58	0.123
Barren	-1.41	0.117	-1.31	0.11
Bog	-2.44	0.154	-2.11	0.133
Conifer	-0.708	0.091	-0.77	0.09
Deciduous	---	---	---	---
Balsam Fir	-0.455	0.112	-0.71	0.11
Disturbed	---	---	---	---
Elevation	-0.44	0.135	-0.42	0.126
Dist. Rivers	---	---	---	---
Dist. Snowmo.	0.24	0.135	0.07	0.144
Dist. Hunters	-0.62	0.135	-0.45	0.124
Hunting Risk	---	---	---	---
Hunting Risk * Protected Area	-0.07	0.552	0.5	0.748
Random Effects	Variance		Variance	
γ (moose)	0.104		2.68	
γHunting Risk	---		---	
γ (Hunting Risk * Protected Area	0.462		3.45	

Figures

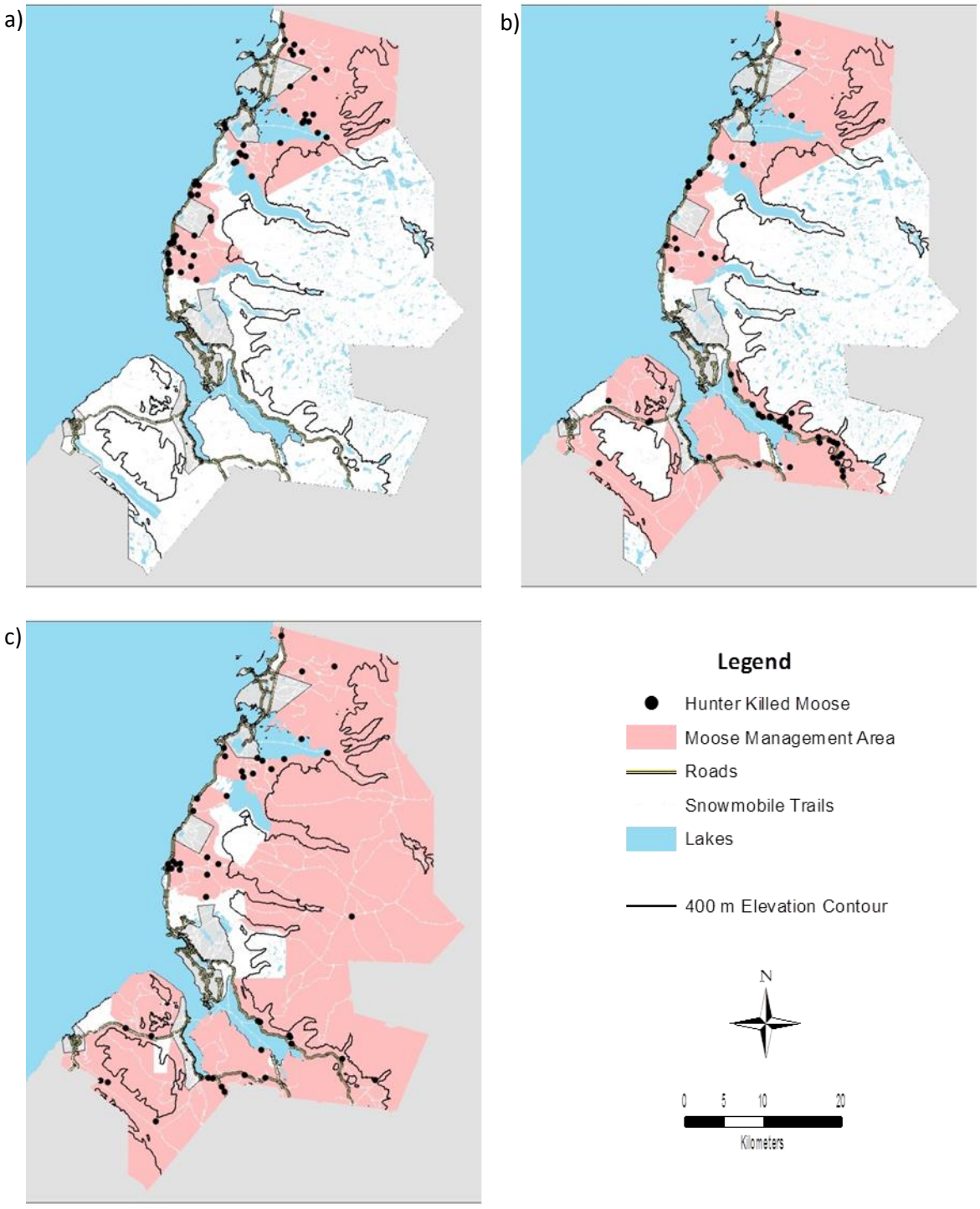

Figure 1: Hunter-killed moose locations in Gros Morne National Park during the: A) 2011 – 2012; B) 2012 – 2013; and, (C) 2013 – 2014 hunting seasons. Sample sizes were *n* = 69, 64 and 60 for 2011 – 2012, 2012 – 2013 and 2013 – 2014, respectively.

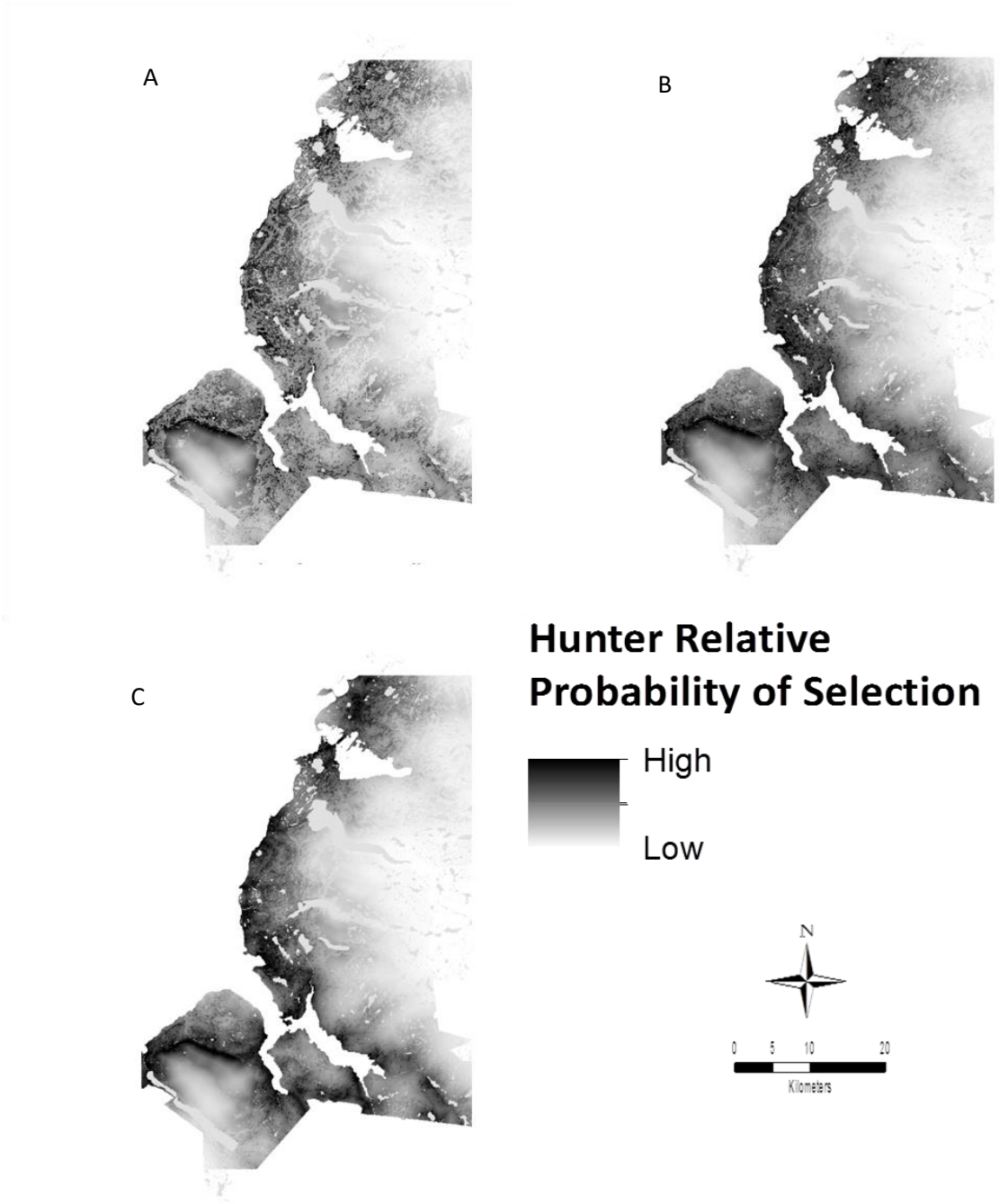

Figure 2: Resource Selection Function Maps based on hunter harvest locations in Gros Morne National Park in: A) 2011– 2012; B) 2012 – 2013; and, (C) 2013 – 2014 hunting seasons. Sample sizes were *n*= 69, 64 and 60 for 2011– 2012, 2012 – 2013 and 2013 – 2014, respectively.

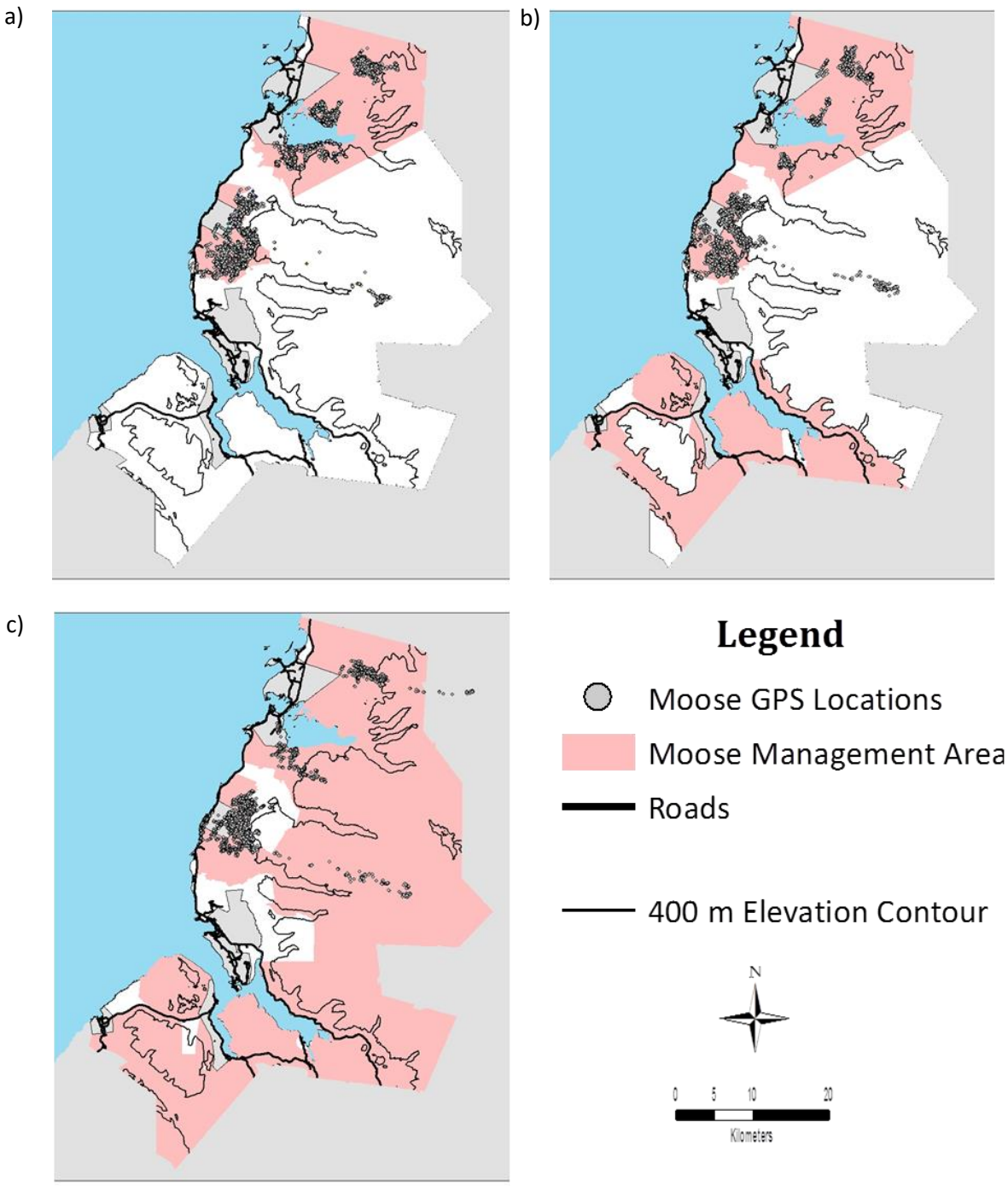

Figure 3: GPS locations taken from *n*= 19, 11, and 7 adult female moose in Gros Morne National Park during the moose hunting season in a) 2011– 12, b) 2012 – 13 and c) 2013 –14, respectively.

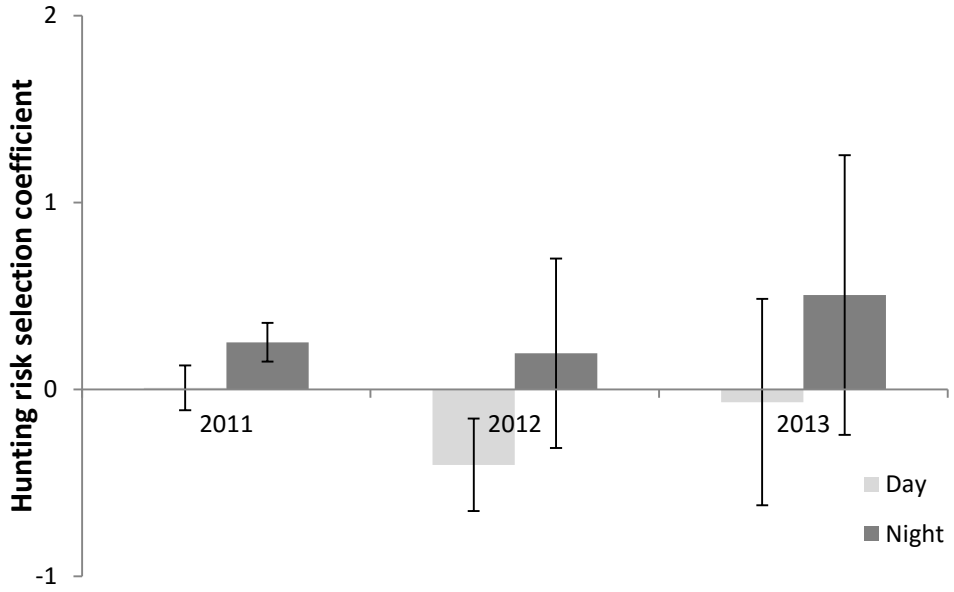

Figure 4: Marginal (population-level) hunting risk selection coefficients (+/- S.E.) for moose estimated by top RSF models taken during day and night during the 2011, 2012 and 2013 hunting seasons in Gros Morne National Park. Differences in hunting risk coefficients suggest patterns of moose selection for hunter risky areas differed between day and night and across years.

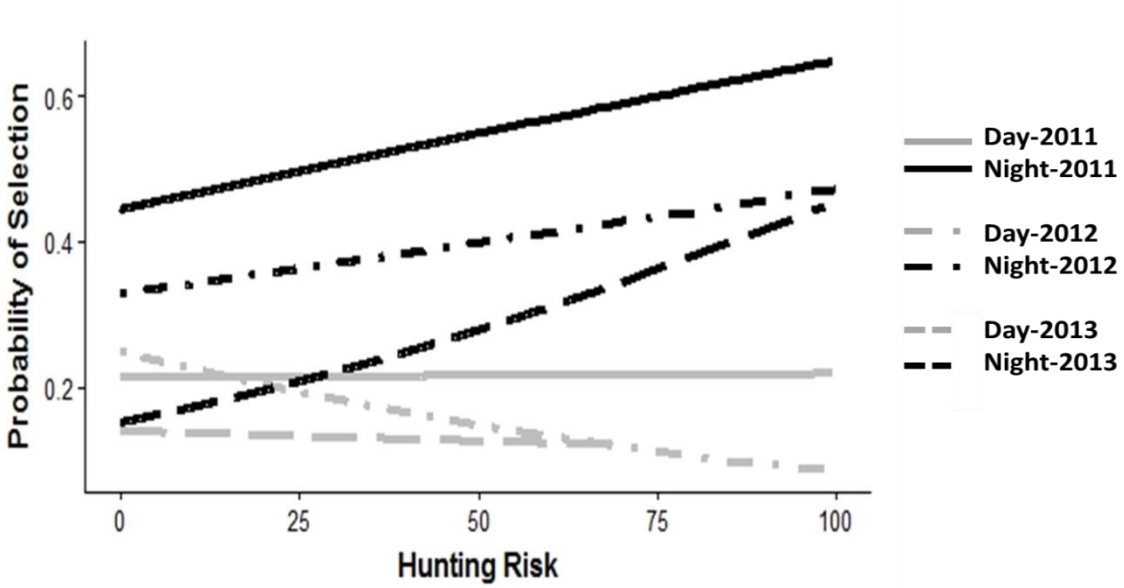

Figure 5: Marginal relative probabilities of selection as a function of hunting risk based on time of day and year for female moose in Gros Morne National Park between the 2011 – 2014 hunting seasons. Predictions were derived from top resource selection function models holding all effects constant, except for response to hunting risk estimates. All probabilities are estimated over hunting risk values estimated for moose according to the corresponding year.

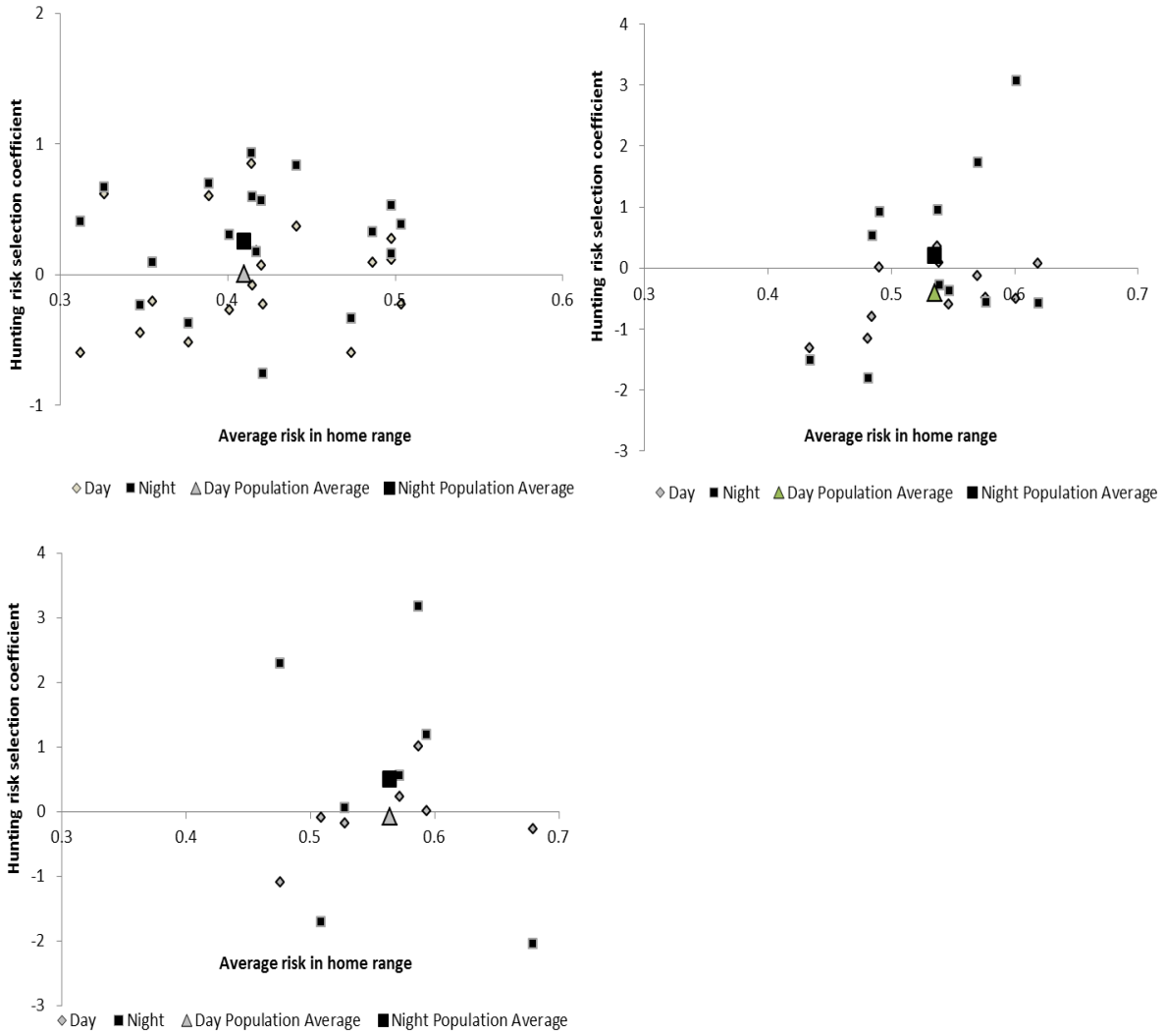

Figure 6: Conditional (individual-level) hunting risk coefficient estimates by moose as a function of hunting risk experienced within the home range during the 2011 – 2012 (*n* = 19), 2012 – 2013 (*n* = 11) and 2013 – 2014 (*n* = 7) hunting seasons in Gros Morne National Park. Selection coefficients for hunting risk were estimated from top RSF models developed during the day and night across three years using generalized linear mixed-models. Individual variation in marginal hunting risk estimates are noticeably different among moose, between day and night, and considerably vary from the conditional (population-level) hunting risk estimates (larger symbols).

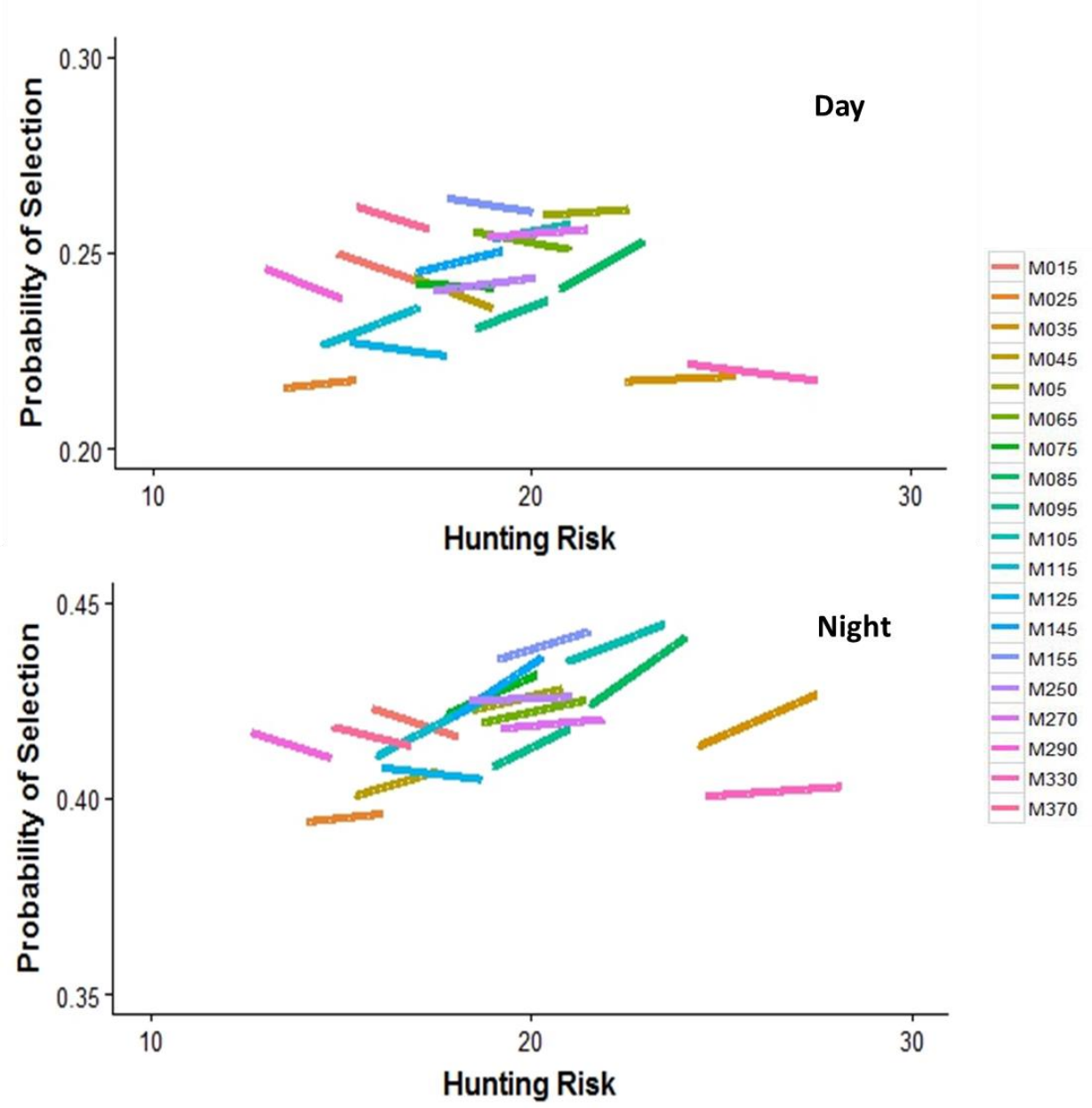

Figure 7: Conditional relative probabilities of selection as a function of hunting risk based on time of day for moose in Gros Morne National Park during the 2011 – 2012 hunting season. Each line (n = 19) represents conditional probabilities of selection made from predictions derived from top resource selection functional models and are conditional on specific moose, holding all other effects constant. All conditional probabilities are estimated over the 95% confidence interval of hunting risk values estimated in each individual's home range. Labeled moose in day-time graphics are intended to highlight the relationship between risk-response and fitness outcomes for individual moose.

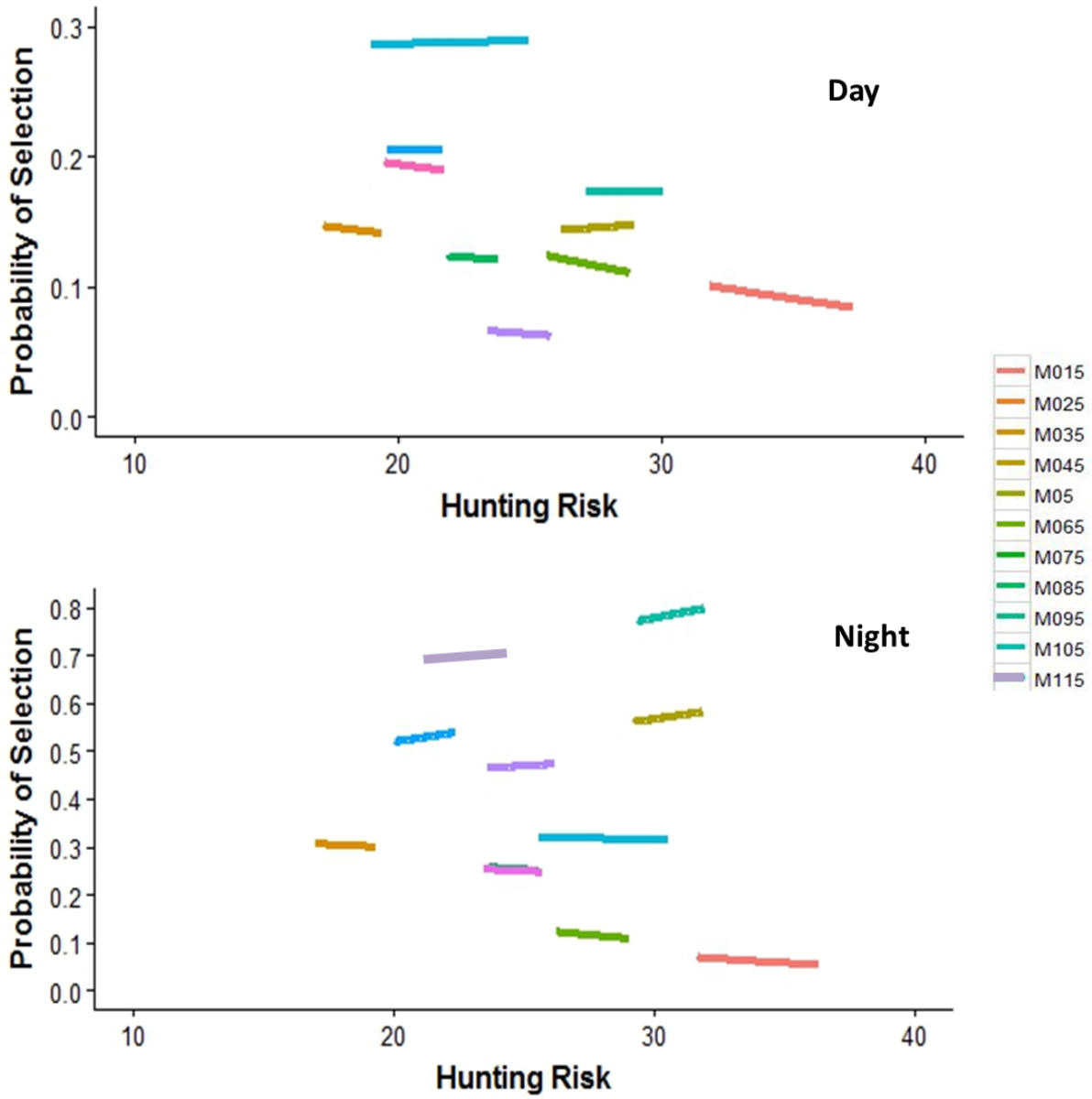

Figure 8: Conditional relative probabilities of selection as a function of hunting risk based on time of day for moose in Gros Morne National Park during the 2012 – 2013 hunting season. Each line (n = 11) represents conditional probabilities of selection made from predictions derived from top resource selection function models and are conditional on specific moose, holding all other effects constant. All conditional probabilities are estimated over the 95% confidence interval of hunting risk values estimated in each individual's home range. Labeled moose in day-time graphics are intended to highlight the relationship between risk-response and fitness outcomes for individual moose.

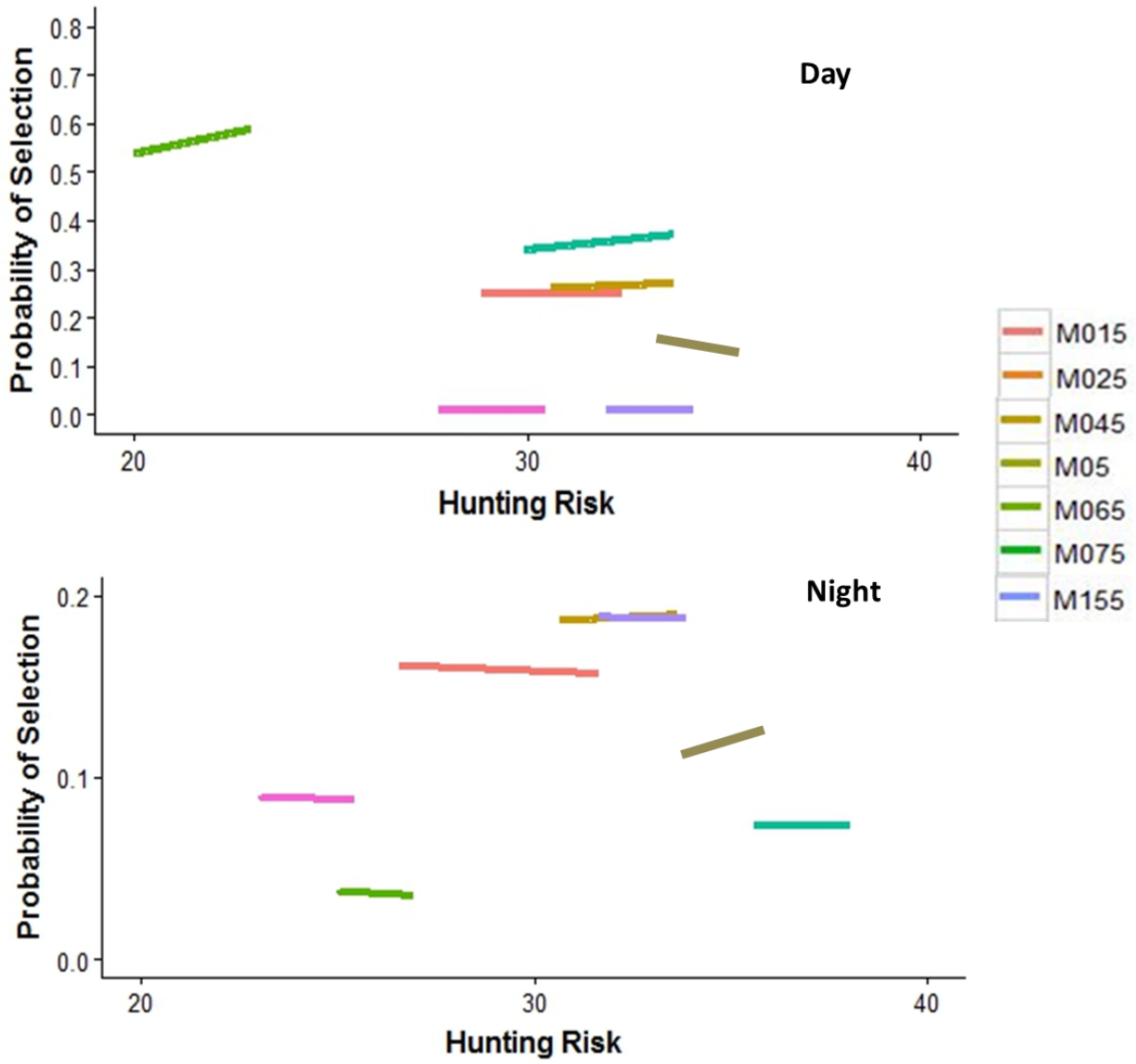

Figure 9: Conditional relative probabilities of selection as a function of hunting risk based on time of day for moose in Gros Morne National Park during the 2013 – 2014 hunting season. Each line (n = 7) represents conditional probabilities of selection made from predictions derived from top resource selection function models and are conditional on specific moose, holding all other effects constant. All conditional probabilities are estimated over the 95% confidence interval of hunting risk values estimated in each individual's home range. Labeled moose in day-time graphics are intended to highlight the relationship between risk-response and fitness outcomes for individual moose.

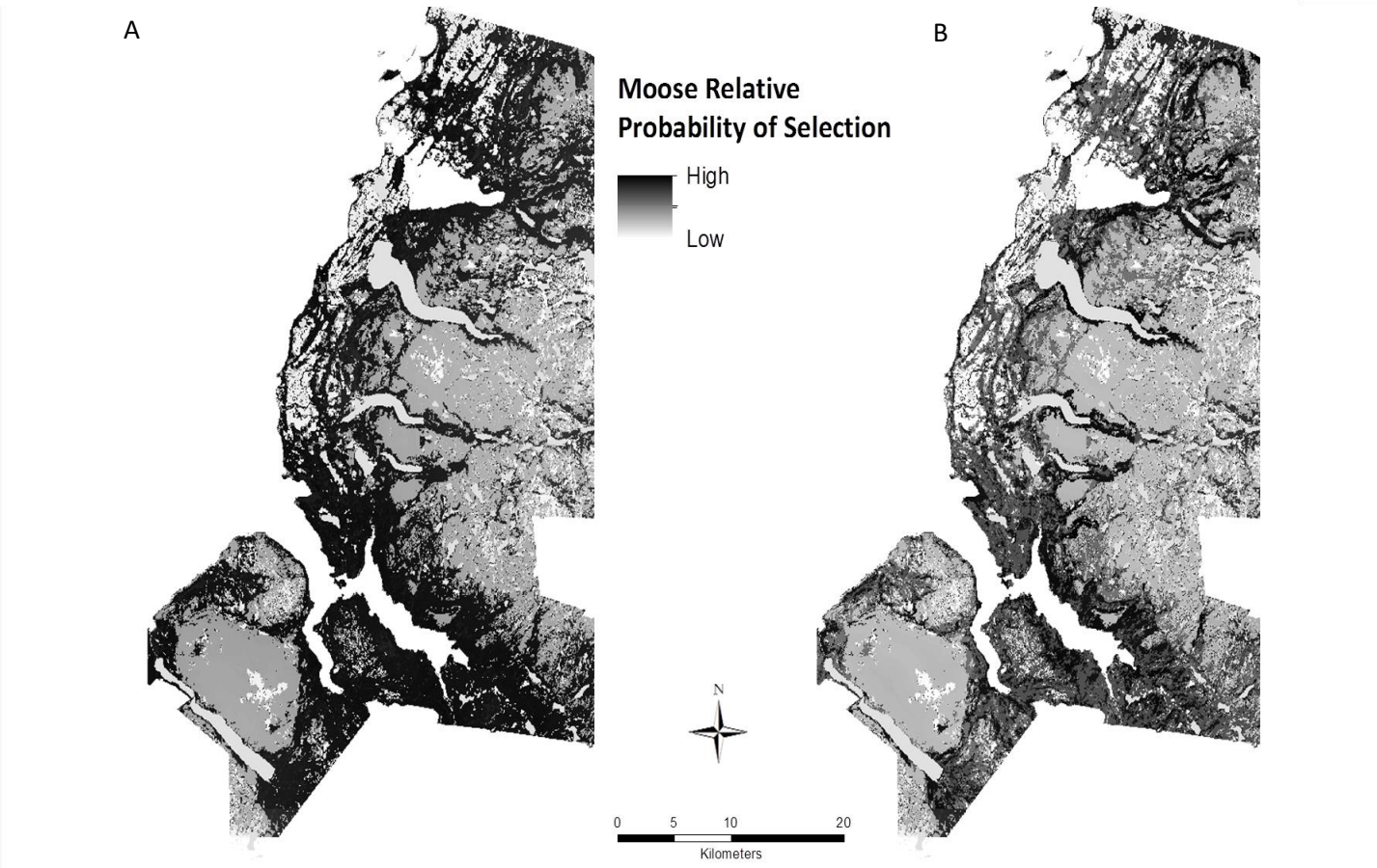

Figure 10: Resource Selection Function Maps for Gros Morne National Park based on GPS collar data collected from female moose during the 2011 – 2012 hunting season during the day (A) and night (B).

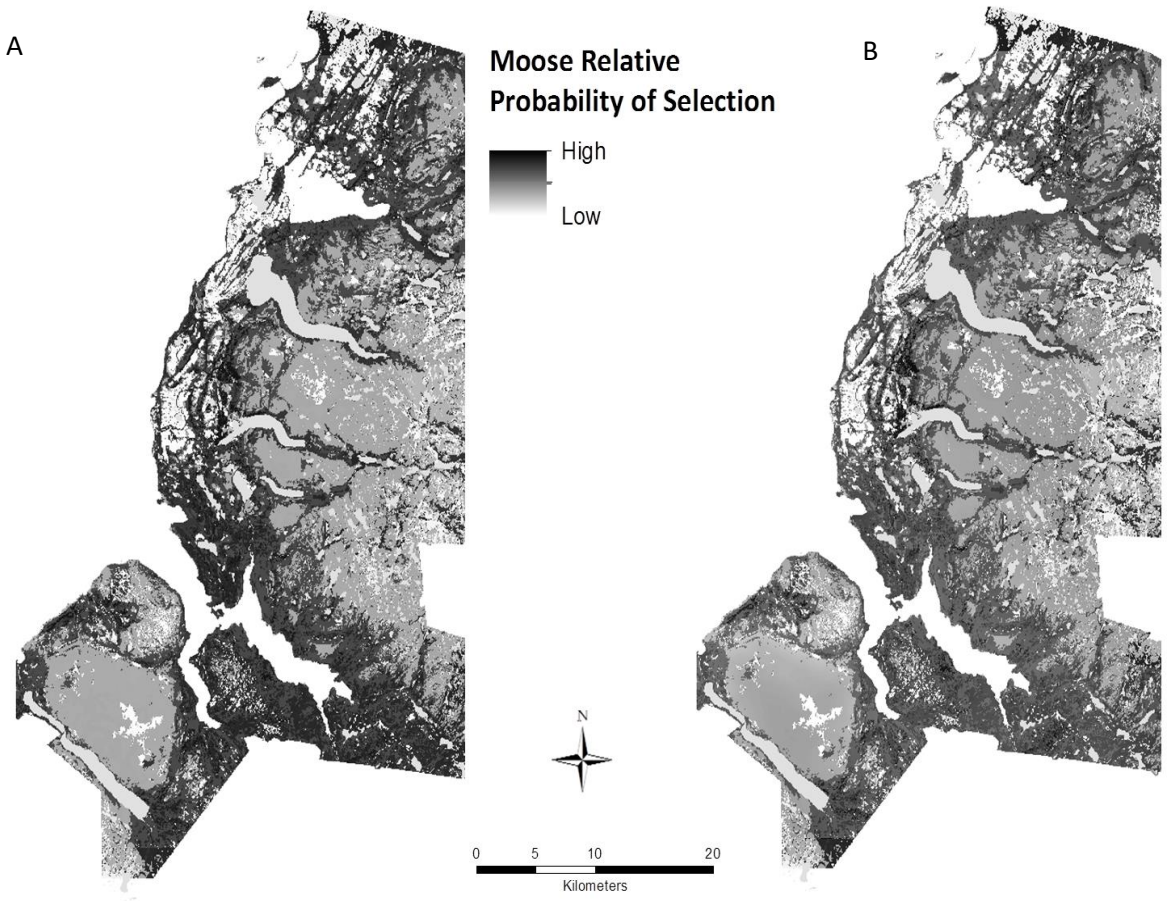

Figure 11: Resource Selection Function Maps for Gros Morne National Park based on GPS collar data collected from female moose during the 2012 – 2013 hunting season during the day (A) and night (B).

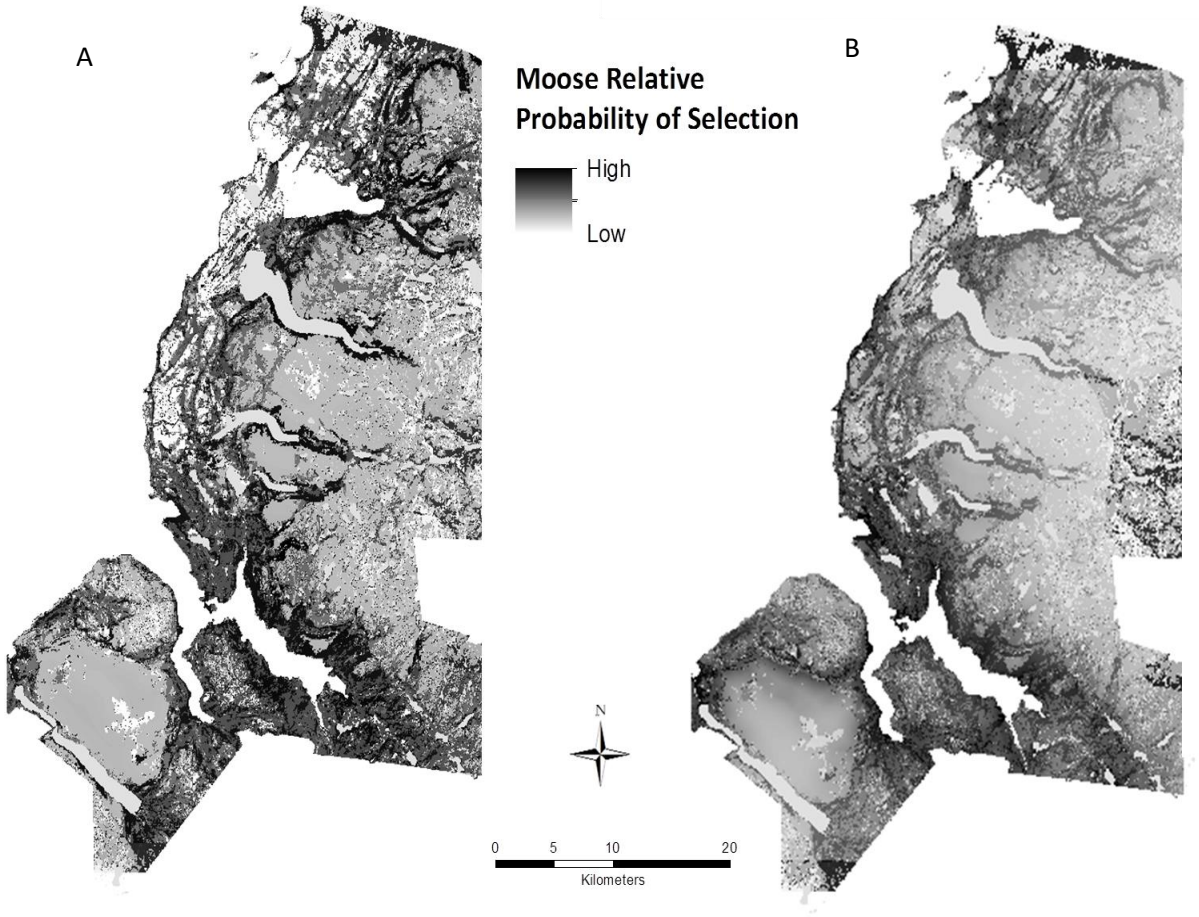

Figure 12: Resource Selection Function Maps for Gros Morne National Park based on GPS collar data collected from female moose during the 2013 – 2014 hunting season during the day (A) and night (B).

LIST OF REFERENCES

Akçakaya, H.R. (2000) Viability analyses with habitat-based metapopulation models. *Population Ecology*, **42**, 45–53.

Barton, K. (2013). MuMIn: Multi-model inference. R package version 1.0. 0. *Vienna, Austria: R Foundation for Statistical Computing. See http://CRAN. R-project. org/package= MuMIn*.

Banfield, C.E. and J.D. Jacobs. (1998) Regional patterns of temperature and precipitation for Newfoundland and Labrador during the past century. *The Canadian Geographer*, **42** (4), 354-364.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2013) lme4: Linear mixed-effects models using Eigen and S4. *R package version, 1*(4).

Beyer, H.L., Jenness, J. & Cushman, S.A. (2010) Components of spatial information management in wildlife ecology: software for statistical and modeling analysis. *Spatial Complexity, Informatics, and Wildlife Conservation* pp. 245–253. Springer.

Blumstein, D.T. & Daniel, J.C. (2005) The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1663–1668.

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F., Hewison, A.M. & Morellet, N. (2014) Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, aru169.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Broders, H. G., Mahoney, S. P., Montevecchi, W. A., & Davidson, W. S. (1999) Population genetic structure and the effect of founder events on the genetic variability of moose, Alces alces, in Canada. *Molecular Ecology*, ***8***(8), 1309-1315.

Brodie, E.D. (1999) Predator-Prey Arms Races Asymmetrical selection on predators and prey may be reduced when prey are dangerous. *Bioscience*, **49**, 557–568.

Brook, R. K. (2010) Habitat selection by parturient elk (Cervus elaphus) in agricultural and forested landscapes. *Canadian Journal of Zoology*, ***88*(10)**, 968-976.

Brown, J. S., & Kotler, B. P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology letters*, ***7,*** 999-1014.

Brown, J.S., Laundré, J.W. & Gurung, M. (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, 385–399.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media.

Christianson, D. & Creel, S. (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology*, **91**, 1184–1191.

Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, **5**, 159–170.

Connor, K. J., Ballard, W. B., Dilworth, T., Mahoney, S., & Anions, D.(2000) Changes in structure of a boreal forest community following intense herbivory by moose. *Alces*, ***36***, 111-132.

Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960–960.

Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.

Cresswell, W., Lind, J. & Quinn, J.L. (2010) Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *Journal of Animal Ecology*, **79**, 556–562.

Cromsigt, J.P., Kuijper, D.P., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I., Mysterud, A., Schmidt, K. & West, K. (2013) Hunting for fear: innovating management of human–wildlife conflicts. *Journal of Applied Ecology*, **50**, 544-549.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani and M. S. Boyce. (2012) Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4407–4416.

Damman, A. W. (1983). An ecological subdivision of the island of Newfoundland. Biogeography and Ecology of the Island of Newfoundland. *W. Junk Publishers*, Boston, Massachusetts, USA, Pages 163-205.

DeCesare, N.J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L. & Musiani, M. (2014) Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, **83**, 343–352.

Dugal, C.J., van Beest, F.M., Vander Wal, E. & Brook, R.K. (2013) Targeting hunter distribution based on host resource selection and kill sites to manage disease risk. *Ecology and Evolution*, **3**, 4265–4277.

Dussault, C., Pinard, V., Ouellet, J.-P., Courtois, R. & Fortin, D. (2012) Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 4481- 4488 .

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Frair, J. L., Merrill, E. H., Allen, J. R., & Boyce, M. S. (2007). Know thy enemy: experience affects elk translocation success in risky landscapes. *The Journal of wildlife management*, ***71***(2), 541-554.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in medicine*, ***27***(15), 2865-2873.

Gervasi, V., Sand, H. akan, Zimmermann, B., Mattisson, J., Wabakken, P. & Linnell, J.D. (2013) Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, **23**, 1722–1734.

Gesch, D.B. (2007) Chapter 4 – The National Elevation Dataset, in Maune, D., ed., Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition: Bethesda, Maryland, American Society for Photogrammetry and Remote Sensing, p. 99-118.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.

Ginsberg, J. R., and E. Milner-Gulland. 1994. Sex biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conservation Biology 8:157–166.

Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, **90**, 699–710.

Gosse, J., Hermanutz, L., McLaren, B., Deering, P. & Knight, T. (2011) Degradation of boreal forests by nonnative herbivores in Newfoundland's national parks: Recommendations for ecosystem restoration. *Natural Areas Journal*, **31**, 331–339.

Hammerschlag, N., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M., Frick, M.G., Godfrey, M.H., Godley, B.J., Griffin, D.B.B., Hartog, K. & others. (2015) Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. *Ecology*, **96**, 2117–2126.

Hebblewhite, M., Merrill, E. H., & McDonald, T. L. (2005) Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos*, ***111*****(1)**, 101-111.

Hebblewhite, M. & Merrill, E. (2008) Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.

Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, ***91*****(05)**, 293-320.

Hosmer, D.W. & Lemeshow, S. (2000) Introduction to the logistic regression model. *Applied Logistic Regression, Second Edition*, 1–30.

Houston, A.I., McNamara, J.M. & Hutchinson, J.M. (1993) General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **341**, 375–397.

Humber, J.M. & Hermanutz, L. (2011) Impacts of non-native plant and animal invaders on gap regeneration in a protected boreal forest. *Biological Invasions*, **13**, 2361–2377.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Joyce, T.L. & Mahoney, S.P. (2001) Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin*, **29**, 281–291.

Karns, P. D. (1998) Population distribution, density and trends. AW Franzmann and CC Schwartz (eds.) –Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, USA*, 125-139.

Kerckhoff, K., McLaren, B.E., Mahoney, S.P. & Knight, T.W. (2013) Moose habitat use throughout Gros Morne National Park. *Alces*, **49**, 113–125.

Kittle, A.M., Fryxell, J.M., Desy, G.E. & Hamr, J. (2008) The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, **157**, 163–175.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the‘ landscape of fear’ in Yellowstone National Park, USA. *Canadian Journal of Zoology*, **79**, 1401–1409.

Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. & Browning, D.M. (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, **95**, 1141–1152.

Laundré, J.W., Hernández, L. & Ripple, W.J. (2010) The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*, **3**, 1–7.

Lebel, F., Dussault, C., Massé, A. & Côté, S.D. (2012) Influence of habitat features and hunter behavior on white-tailed deer harvest. *The Journal of Wildlife Management*, **76**, 1431–1440.

Lima, S.L. & Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lone, K., Loe, L.E., Meisingset, E.L., Stamnes, I. & Mysterud, A. (2015) An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*, **102**, 127–138.

Lyon, L.J. & Burcham, M.G. (1998) *Tracking Elk Hunters with the Global Positioning System*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Manly, B.F. (2002) *Statistics for Environmental Science and Management*. Taylor & Francis.

McLaren, B., McCarthy, C., Mahoney, S. (2000) Extreme moose demographics in Gros Morne National Park, Newfoundland. *Alces*, **36**, 217-232.

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., & Contasti, A. L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, ***79***(1), 4-12.

McLoughlin, P. D., Boyce, M. S., Coulson, T., & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society of London B: Biological Sciences*, ***273***(1593), 1449-1454.

Meades, W.J., Moores L. (1989). Forest site classification manual: a field guide to the Damman forest types of Newfoundland. Forestry Canada, Canada.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, ***4***(2), 133-142.

Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Jimenez, M.D., Cook, R.C., Cook, J.G., Albeke, S.E., Sawyer, H. & White, P.J. (2013) Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology letters*, **16**, 1023–1030.

Neumann, W., Ericsson, G. & Dettki, H. (2009) The non-impact of hunting on moose Alces alces movement, diurnal activity, and activity range. *European journal of wildlife research*, **55**, 255–265.

Nicholson, K.L., Milleret, C., Maansson, J. & Sand, H. akan. (2014) Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. *Oecologia*, **176**, 69–80.

Orrock, J.L., Grabowski, J.H., Pantel, J.H., Peacor, S.D., Peckarsky, B.L., Sih, A. & Werner, E.E. (2008) Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. *Ecology*, **89**, 2426–2435.

Padié, S., Morellet, N., Hewison, A.J., Martin, J.-L., Bonnot, N., Cargnelutti, B. & Chamaillé-Jammes, S. (2015) Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos*, **124**, 1536–1546.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.

Preisser, E.L., Bolnick, D.I. & Grabowski, J.H. (2009) Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecology letters*, **12**, 315–323.

Proffitt, K.M., Grigg, J.L., Garrott, R.A., Hamlin, K.L., Cunningham, J., Gude, J.A. & Jourdonnais, C. (2010) Changes in Elk Resource Selection and Distributions Associated With a Late-Season Elk Hunt. *The Journal of Wildlife Management*, **74**, 210–218.

Proffitt, K.M., Grigg, J.L., Hamlin, K.L. & Garrott, R.A. (2009) Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *The Journal of Wildlife Management*, **73**, 345–356.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Review of Ecology and Systematics*, 523–575.

Rae, L.F., Whitaker, D.M. & Warkentin, I.G. (2013) Multiscale impacts of forest degradation through browsing by hyperabundant moose (Alces alces) on songbird assemblages. *Diversity and Distributions*, **20**, 382-395.

Ripple, W.J. & Beschta, R.L. (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience*, **54**, 755–766.

Ripple, W.J. & Beschta, R.L. (2012) Trophic cascades in Yellowstone: The first 15years after wolf reintroduction. *Biological Conservation*, **145**, 205–213.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, ***82***(2), 291-318.

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006) Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1421–1427.

Smith, D.W., Peterson, R.O. & Houston, D.B. (2003) Yellowstone after wolves. *BioScience*, **53**, 330–340.

Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C. & Baubet, E. (2009) Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology*, **87**, 1129–1137.

Van Beest, F. M., Vander Wal, E., Stronen, A. V., Paquet, P. C., & Brook, R. K. (2013) Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. *Oecologia*,**173(2)**, 409-420.

Vander Wal, E. & Rodgers, A.R. (2012) An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, **224**, 48–53.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.

Wirsing, A.J. & Heithaus, M.R. (2014) Accounting for individual behavioural variation in studies of habitat selection. *Journal of Animal Ecology*, **83**, 319–321.

APPENDIX A

Table A1: Results of model selection for years 1, 2 and 3 mixed-effects resource selection models based on female moose GPS collar data over the first three years of hunting (2011 – 2014) in Gros Morne National Park, showing model name, structure, random coefficients and intercepts, Δ AICc and conditional coefficient of determination (R^2C) scores. Top Models are highlighted in bold.

Model Name	Structure	Random Coefficient	Random Intercept	ΔAICc
Year-1 Day Model				
Hunting Risk	Hunting Risk	1	Moose ID	645
Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	56
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	57
Anthropogenic	Used~ Dist. Hunters + Dist. Snowmo. + Dist. Roads + Disturbed	1	Moose ID	709
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	52
Best Naïve Model	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters	1	Moose ID	48
Best Naïve Model + Hunting Risk	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk	1	Moose ID	50
Best Naïve Model + Hunting Risk*In Hunt Zone	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk * In Hunt Zone	1	Moose ID	41
Best Model + Random Hunting Coefficient	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk	Hunting Risk	Moose ID	0
Best Model + Random Hunting*In Hunt Zone	Barren + Bog + Conifer + Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	VIF > 5

Year-1 Night Model				
Hunting Risk	Hunting Risk	1	Moose ID	399
Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	92
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	56
Anthropogenic	Used~ Dist. Hunters + Distr. Snowmo. + Dist. Roads + Disturbed	1	Moose ID	386
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	89
Best Naïve Model	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers	1	Moose ID	65
Best Naïve Model + Hunting Risk	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers Hunting Risk	1	Moose ID	45
Best Naïve Model + Hunting Risk*In Hunt Zone	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	1	Moose ID	41
Best Model + Random Hunting Coefficient	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers Hunting Risk	Hunting Risk	Moose ID	0
Best Model + Random Hunting*In Hunt Zone	Balsam Fir + Barren + Bog + Conifer + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	VIF > 5
Year-2 Day Model				
Hunting Risk	Hunting Risk	1	Moose ID	622

Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	83
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	81
Anthropogenic	Used~ Dist. Hunters + Dist. Snowmo + Dist. Roads + Disturbed	1	Moose ID	576
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	86
Best Naïve Model	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers	1	Moose ID	81
Best Naïve Model + Hunting Risk	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk	1	Moose ID	80
Best Naïve Model + Hunting Risk*In Hunt Zone	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	1	Moose ID	66
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk	Hunting Risk	Moose ID	35
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Deciduous + Disturbed + Dist. Rivers + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0

Year-2 Night Model

Hunting Risk	Hunting Risk	1	Moose ID	492
Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	128
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	129

Anthropogenic	Used~ Dist. Hunters + Snowmo + Dist. Roads + Disturbed	1	Moose ID	379
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	132
Best Naïve Model	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers	1	Moose ID	124
Best Naïve Model + Hunting Risk	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers * Hunting Risk	1	Moose ID	126
Best Naïve Model + Hunting Risk*In Hunt Zone	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers +Hunting Risk * In Hunt Zone	1	Moose ID	123
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers * Hunting Risk	Hunting Risk	Moose ID	60
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Disturbed + Dist. Rivers +Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0
Year-3 Day Model				
Hunting Risk	Hunting Risk	1	Moose ID	779
Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	200
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	201
Anthropogenic	Used~ Dist. Hunters + Snowmo + Dist. Roads + Disturbed	1	Moose ID	527
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	196
Best Naïve Model	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo.	1	Moose ID	193

Best Naïve Model + Hunting Risk	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk	1	Moose ID	195
Best Naïve Model + Hunting Risk*In Hunt Zone	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk * In Hunt Zone	1	Moose ID	187
Best Model + Random Hunting Coefficient	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters + Dist. Snowmo. +Hunting Risk	Hunting Risk	Moose ID	170
Best Model + Random Hunting*In Hunt Zone	Balsam.Fir + Barren + Bog + Conifer + Elevation + Dist. Hunters +Dist. Snowmo. + Hunting Risk * In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0

Year-3 Night Model				
Hunting Risk	Hunting Risk	1	Moose ID	668
Natural	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers	1	Moose ID	146
Natural + Hunting Risk	Barren + Bog + Conifer + Disturbed + Deciduous + Elevation + Dist. Rivers + Hunting Risk	1	Moose ID	142
Anthropogenic	Used~ Dist. Hunters + Snowmo + Dist. Roads + Disturbed	1	Moose ID	400
Naïve Global Model	Barren + Bog + Conifer + Disturbed + Deciduous +Disturbed + Elevation + Dist. Rivers + Dist. Hunters + Dist. Snowmo.	1	Moose ID	129
Best Naïve Model	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo.	1	Moose ID	125
Best Naïve Model + Hunting Risk	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk	1	Moose ID	125
Best Naïve Model + Hunting Risk*In Hunt Zone	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk * In Hunt Zone	1	Moose ID	111

Best Model + Random Hunting Coefficient	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk	Hunting Risk	Moose ID	105
Best Model + Random Hunting*In Hunt Zone	Barren + Bog + Decid + Disturbed + Elevation + Dist. Hunters + Dist. Snowmo. + Hunting Risk In Hunt Zone	Hunting Risk * In Hunt Zone	Moose ID	0

*High variance inflation factor (VIF) scores are thought to be due to low sample sizes outside of hunting area.